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REVISION OF TITHONIA

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ABSTRACT. *Tithonia* Desf. ex Gmelin is a genus distributed primarily in Mexico and Central America. The present treatment recognizes 13 taxa in 11 species, arranged in two sections. Chromosome counts are reported for 51 populations for 12 taxa of *Tithonia*. The genus is diploid at $n = 17$, with two taxa, *T. koelzii* McVaugh and *T. calva* var. *auriculata* La Duke, having B chromosomes. Numerical phenetics were used to help evaluate the morphological variation among the taxa. Fifty-eight characters were measured and evaluated using both cluster analysis and principal component analysis. These analyses resulted in a better understanding of subgeneric, specific, and subspecific groups. Phylogenetic reconstruction techniques were then used to develop hypotheses about the evolutionary relationships among the taxa. Using the phenetic and phylogenetic analyses, a subgeneric classification was proposed consisting of two sections, one of which has three series.

Collectors of Compositae in Mexico and Central America are usually familiar with the large, yellow or orange-rayed members of the genus *Tithonia*. Many species are weedy and sometimes dominate cultivated or fallow fields. Some taxa, such as *Tithonia diversifolia* (Hemsl.) A. Gray and *T. rotundifolia* (Mill.) S. F. Blake, are grown as ornamentals for their bushy stature and show of brilliantly colored flowers. The genus contains both annuals and perennials, and was last revised by Blake (1921) to include 10 species. Since that time, three taxa have been described, *T. pedunculata* Cronquist (Cronquist, 1965), *T. koelzii* McVaugh (McVaugh, 1972) and *T. hondurensis* LaDuke (LaDuke, 1982). Blake's (1921) revision was restricted to herbarium material and provided little insight into the evolutionary relationships among the taxa. The present study utilizes herbarium material, field observations, cytology, and numerical phenetics and cladistics, to provide data not only for a revision of the genus, but also for developing evolutionary hypotheses.

TAXONOMIC HISTORY

Tithonia was first described by Jussieu (1789). Jussieu referenced a presentation by Desfontaine which was to be published in Act. Paris extr. Vol. 12, but never appeared (Stafleu & Cowan, 1976; Desfontaine eventually did publish a generic description of *Tithonia* with the species *T. tagetiflora,* but not until 1802). Gmelin (1791) also cited this presentation of Desfontaine, and provided an additional generic description and a specific name, *T. uniflora.* The type species for the genus, *T. uniflora* Gmelin, however, must be called *Tithonia rotundifolia* (Miller) S. F. Blake, because *Tagetes rotundifolia* Miller (1768) is an earlier name for the same taxon.

Subsequently, a number of taxa in *Tithonia* were described and generic rearrangements made. In 1836, DeCandolle, in the Prodromus, recognized four species of *Tithonia.* Two of these, *T. pachycephala* DC. and *T. excelsa* (Willd.) DC., are now recognized as belonging to *Viguiera* (Blake, 1918). Schultz, in Seemann's Botany of the Voyage of the Herald (1856), described the subgenus *Mirasolia* to include the new taxon, *T. calva* Sch.-Bip. in Seemann. The subgenus *Mirasolia,* with two taxa, was proposed for generic status by Bentham and Hooker (1873), and all of *Tithonia* had four taxa. W. B. Hemsley (1881) recognized three taxa of *Mirasolia* and eight of *Tithonia.* Kuntze (1891) used the new generic name, *Urbanisol* (named after Dr. Ignaz Urban), and it included many of the taxa of *Tithonia.* This arrangement was proposed because he was a believer in absolute priority, and the name *Tithonia* had been used already by Linneaus in 1737 for *Rivina* L. (Phytolacaceae). He also retained *Mirasolia.* Blake (1918) moved a number of taxa of *Gymnolomia* into *Tithonia* and revised the genus in 1921, recognizing ten species and two subspecies.

In the present revision of *Tithonia,* I recognize many of the taxa of Blake (1921), the two new taxa described by McVaugh and Cronquist, and one recently described taxon. This gives eleven species (thirteen taxa) in two sections, as shown below:

Section *Tithonia*
- *Series Tithonia*
  - *Tithonia brachypappa* B. L. Robinson
  - *Tithonia rotundifolia* (Miller) S. F. Blake
  - *Tithonia thurberi* A. Gray

Tithonia tubaeformis (Jacq.) Cass.
Series *Fruticosae* La Duke
Tithonia fruticosa W. M. Canby & J. N. Rose in J. N. Rose
Tithonia pendunculata A. Cronquist
Series *Grandiflorae* La Duke
Tithonia diversifolia (Hemsl.) A. Gray
Tithonia koelzii R. McVaugh
Section *Mirasolia* (Sch.-Bip. in Seemann) La Duke
Tithonia calva var. *calva* Sch.-Bip. in Seemann
Tithonia calva var. *auriculata* (Brandegee) La Duke
Tithonia calva var. *lancifolia* (B. L. Robinson & Greenm.) McVaugh
Tithonia hondurensis La Duke
Tithonia longiradiata (Bertol.) S. F. Blake

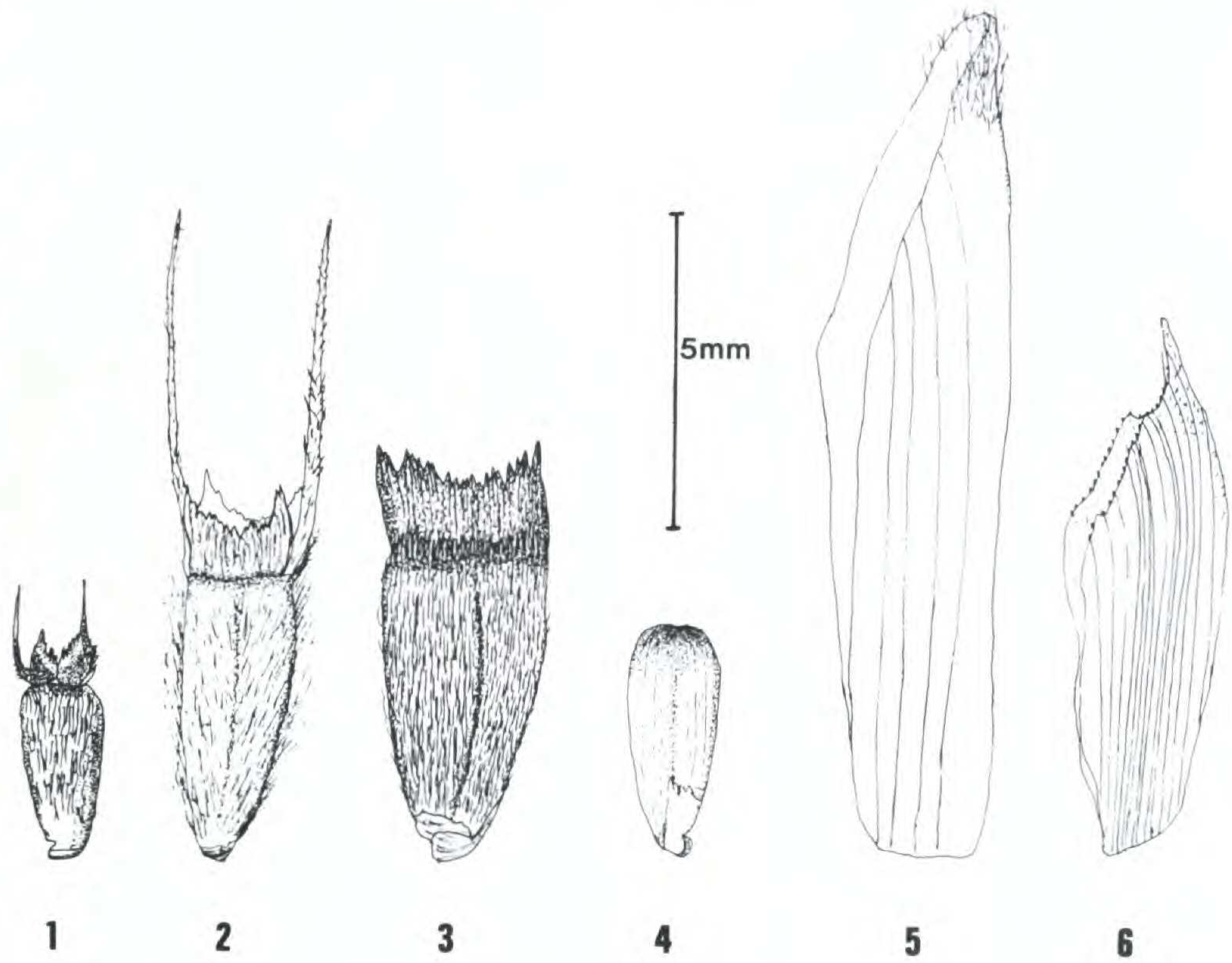
GENERIC AND SUBTRIBAL RELATIONSHIPS

Cassini (1829) placed *Tithonia* in the "Hélianthées section Rudbeckiées," with genera bearing superficial similarities (e.g. *Echinacea*). Lessing (1832) placed a number of the genera currently accepted as members of the Heliantheae in one of two tribes, "Senecionideae" or "Asteroideae." *Tithonia* was in the "Senecionideae subtribe Heliantheae [subdivision] Coreopsideae." The genera *Helianthus* L. and *Viguiera* H.B.K. were first allied to *Tithonia* at this time. DeCandolle (1836) followed Lessing (1832) at the tribal and subtribal level, but he added a number of taxa to his "Division Coreopsideae" which included *Tithonia*, *Viguiera*, and *Helianthus*. Bentham & Hooker (1873) recognized the tribe Helianthoideae, with ten subtribes, including Subtribe Verbesineae which, among other genera, contained *Gymnolomia*, *Helianthus*, *Mirasolia*, *Tithonia*, and *Viguiera*. Hoffmann (1890) followed this same basic concept. Stuessy (1977) recognized the legitimate subtribal name Helianthinae Dumort (Solbrig, 1963) for the group including *Helianthus*. This subtribe also retains *Gymnolomia* H.B.K., *Tithonia*, and *Vigueria* as members. The Verbesininae are suggested to include taxa close to *Verbesina* L.

The genera historically most closely related to *Tithonia* are *Gymnolomia*, *Helianthus*, and *Viguieria*. Some of the taxa in *Gymnolomia* were considered more than closely related to *Tithonia* by Blake

(1918), because he transferred many of them to *Tithonia*. Following these transfers, and others by Blake (1918), the genus *Gymnolomia* was reduced to four taxa, and no longer considered a close relative. Taxa of the genus *Helianthus* share similarities with some taxa of *Tithonia* such as habit, achene shape, and achene pubescence. *Helianthus*, however, produces a pappus of two awns which are readily deciduous, whereas *Tithonia* either does not produce a pappus or produces a nondeciduous pappus of a different nature. Other characters, such as the shape of the receptacle in fruit, which is convex in *Tithonia* and mostly flat in *Helianthus*, and the phyllary shape, linear to spathulate in *Tithonia* and usually obspathulate in *Helianthus*, further differentiate the two genera.

Blake (1918, p. 10) stated that the "origin of *Tithonia* as a Central American offshoot of some lost Viguieroid stock related to (subgenus) *Amphilepis* is more than probable." There are a number of large-headed taxa in subgenus *Amphilepis* and subgenus *Calanticaria* section *Hypargyrea*, which approach *Tithonia*. These taxa, which can be considered closely related to *Tithonia*, are *Viguiera excelsa* (Willd.) B. & H., *V. angustifolia* (H. & A.) S. F. Blake, *V. pachycephala* (DC.) Hemsl., *V. decurrens* A. Gray, *V. rosei* Greenm., and *V. hypargyrea* Greenm. The best character for differentiating these taxa from *Tithonia* is the nature of the peduncle. Penuncles of these *Viguiera* taxa may be thickened (e.g., *Viguiera excelsa, V. hypargyrea*), but they are cylindrical or angulate, and usually filled with pith. Another character differentiating these taxa is the nature of the pappus (Fig. 1–4.) Taxa such as *V. excelsa* and *V. pachycephala* are characterized by two awns and 4–10 scales (Fig. 1). These scales tend to be separate in these species, while in *Tithonia* the taxa are either without or with a pappus (Figs. 2–4). Of the latter, two types of pappus occur. First, a ring of basally and laterally fused squamellae occurs in *T. brachypappa* (sometimes reduced), *T. fruticosa*, and *T. koelzii* (Fig. 3). Second, awns are present, but again the squamellae are fused at least basally (Fig. 2). Taxa such as *V. decurrens, V. hypargyrea*, and *V. rosei* can be differentiated by the nature of the apex of the pales. The tip in these taxa is truncate and cupped, whereas those in *Tithonia* have acute to aristate-tipped pales (Figs. 5 & 6). Therefore, a number of characters are important in differentiating *Tithonia* taxa from its closest *Viguiera* relatives: 1) the flared (fistulose) hollow peduncle, 2) the nature of the pappus, and 3) the nature of the pales.



Figures **1–6**. Achenes (Figs. 1–4) and pales (5 & 6) of *Viguiera* and *Tithonia*. **1**, *V. excelsa (Cronquist 9791*, TEX); **2**, *T. tubaeformis (La Duke et al. 406*, OS); **3**, *T. fruticosa (Weber & Bye 8352*, voucher grown from seed, OS); **4**, *T. calva* var. *calva (Cronquist 10550*, MICH); **5**, *V. rosei (McVaugh 896*, OS); **6**, *calva* var. *calva (Cronquist 10550*, MICH). All same scale.

CYTOLOGY

Chromosome numbers from the taxa of *Tithonia* were determined for either mitotic or meiotic material using standard techniques of killing, fixing, and staining (Snow, 1963; Stuessy, 1971; Jackson, 1973).

Twelve of the thirteen taxa of *Tithonia* have been examined from 51 populations. Five taxa are reported here for the first time. Most populations are $n = 17$ ($2n = 34$), but variation does occur (Table 1), primarily in the presence of B-chromosomes. *Tithonia calva* var. *auriculata* preparations had $2n = 34 + 4$B's, while the B-complement in *T. koelzii* varied from 4 to 5 per cell in addition to the normal complement. In previous studies of B-chromosomes, correlations were made between the number of B's with adaptation to climate (Frost, 1958), stress (Rees & Hutchinson, 1973), and chiasmata fre-

Table 1. Chromosome numbers in *Tithonia*.

Taxon	Chromosome Number *n*	2n	Number of Populations Sampled, and/or Reference
T. brachypappa	17[a]		3[b]
T. calva var. *calva*	17		3; Solbrig et al. 1972, (as *T. auriculata;* Keil & Pinkava, 1976.
		34	1; Turner & Flyr, 1966.
T. calva var. *auriculata*		34+4B[a]	1
T. diversifolia	17		5; Powell & King, 1969; Solbrig et al., 1972.
	15		Mehra & Remanandan, 1969.
		34	Turner, Ellison & King, 1961.
T. fruticosa		34[a]	1
T. hondurensis	17[a]		1
		34[a]	1
T. koelzii	17+6B[a]		1
		34+5B[a]	1
T. longiradiata	17		3
		34	Turner, Powell, & King, 1962; Turner, Ellison, & King, 1961
T. pedunculata	17		1; Solbrig et al., 1972.
		34	1
T. rotundifolia	17		5; Subramanyam & Kamble, 1967; Sarkar et al., 1978; Gupta & Gill, 1979.
		34	5; Turner & King, 1964; Bilquez in Delay, 1951; Heiser, 1948.
		32	Vilmorin & Chopinet, 1954.
T. thurberi	17		Keil & Powell, 1976.
		34	1
T. tubaeformis	17		12; Solbrig et al., 1972; Keil & Stuessy, 1977.
	ca.17		1
		34	6; Turner & Johnston, 1961; Turner, Ellison, & King, 1961; Heiser & Smith, 1955.

[a] *First report*

[b] *Populations sampled are labeled with an asterisk (*) in the representative specimen section following each taxon.*

quency (Cameron & Rees, 1967; Vosa & Barlow, 1972). Due to the limited material of both of these taxa, correlations of this sort have not been possible. Therefore, the role that B-chromosomes have played in the speciation and evolution of the taxa is difficult to assess.

The taxa in *Viguiera* most closely related to *Tithonia* are unknown cytologically. The base number, however, for the genus is $n = 8$ or 17 (Jansen & Stuessy, 1980), with most of the taxa being $n = 17$. Similarly, *Helianthus* is based on $n = 17$. These data are not useful, therefore in differentiating *Tithonia* from these genera, but they do indicate a close tie among all three.

ISOLATING MECHANISMS

The absence of polyploidy in *Tithonia* suggests that speciation has occurred only at the diploid level. Isolating mechanisms that are operating to preserve the species in *Tithonia* are primarily of two types: 1) spatial isolation and 2) reproductive isolation (Levin, 1978). Spatial isolation is probably the primary mode, with most of the taxa occurring in areas geographically isolated from each other. In most cases of geographical overlap, the taxa are isolated by habitat differences. Two pairs of taxa have been collected sympatrically: *T. diversifolia* with *T. longiradiata*, and *T. tubaeformis* with *T. rotundifolia*. The population of *T. diversifolia* and *T. longiradiata (La Duke et al. 535 & 536)* in Guatemala had no detectable intermediates. The exact mode of reproductive isolation is not clear. However, since no F_1 hybrids were detected and these taxa flower at the same time, the isolating mechanism has been narrowed to one of the following modes (from Levin, 1978): 1) Floral divergence, 2) reproductive mode, 3) cross-incompatibility, or 4) hybrid inviability or weakness. None of these can be eliminated at this time, as any of them are equally probable.

Isolation in the second pair of sympatric species, *Tithonia tubaeformis* and *T. rotundifolia* is somewhat easier to explain. Samples from two mixed populations (*La Duke et al. 510, & 511; Stuessy & Gardner 4093, & 4094*) indicate that hybridization to the F_1 level has occurred. Pollen stainability using lactophenol cotton blue (Hauser & Morrison, 1964) showed a putative hybrid from *La Duke et al. 510* and *511* with 23% stainable pollen (200 grains sampled). Parental pollen was 98.5% for *T. rotundifolia* and 99% for *T. tubaeformis*.

The isolating mechanism in this case, therefore, is hybrid sterility, a mode frequently encountered in interspecific crosses (Levin, 1978).

CONCEPTS OF SPECIES, VARIETIES, AND SECTIONS

The species concept used in this study is a phenetic one (Sokal and Crovello, 1970). No data are available, other than those mentioned above, concerning the crossability of the taxa, so a biological species concept (Mayr, 1963) cannot be utilized totally. However, the genetic isolation cited above does support a biological species concept. The numerical taxonomic study, to be discussed later, demonstrates two important ideas: (1) the taxa of *Tithonia,* as represented by populational samples, are cohesive groups; and (2) these cohesive taxa are well differentiated from each other using morpological criteria.

Both subspecies and variety are frequently used as subspecific categories in botanical systematic studies. Historically, however, there has been less distinction between taxa at the varietal rank than between taxa at the subspecific rank (Kapadia, 1963; Burtt, 1970). The amount of differentiation between the three subspecific taxa in *T. calva* is relatively small, but geographically consistent; therefore, the rank of variety has been chosen to indicate this minor difference.

Sections are used instead of subgenera in this treatment because the differences between the two main groups of taxa in *Tithonia* are believed to be less than those reflected ordinarily by the rank of subgenus.

NUMERICAL TAXONOMY

Historically, *Tithonia* is a relatively small group of taxa (10 species recognized by Blake, 1921). However, there is confusing morphological diversity in some parts of the genus at both the populational and specific levels. First, two taxa, *T. diversifolia* and *T. rotundifolia,* are quite similar in a number of features and these have been misidentified in a number of recent publications (Pal et al., 1976; Herz & Sharma, 1975). Second, one of Blake's (1921) species, *T. auriculata,* is difficult to distinguish from *T. calva* var. *lancifolia,* differing primarily in morphology of the leaves. Third, a number of populations of *T. longiradiata* in Honduras and Belize are different in having smaller heads, and strongly revolute leaf margins, and may represent a different species. Fourth, there have been no clearly defined subgeneric groups to help provide a better understanding of the most closely related taxa.

To assist in resolving the taxonomic problems mentioned above, methods of computer-assisted numerical taxonomy were used. Earlier workers have suggested that the use of numerical techniques should be part of routine taxonomic studies (e.g., Gilmartin & Harvey, 1976). The concept of numerical taxonomy has progressed from simple comparisons of similarities and differences to more sophisticated multivariate techniques (for a review, see Sneath & Sokal, 1973). Numerical techniques can be useful in understanding the distribution and amount of variation of morphological characteristics (McNeill, 1979). Methods such as clustering or principal component analysis (PCA) can assist in developing taxonomic concepts, but they do not themselves define the subgeneric, specific, or subspecific boundaries. Each analysis must be carefully interpreted, and can only serve as a guideline in taxonomic delimitations.

The purpose of this section is to summarize the similarities and differences among the taxa to determine particularly: 1) the morphological integrity of *Tithonia diversifolia, T. longiradiata,* and *T. rotundifolia,* 2) the relationships of *T. auriculata* to *T. calva* var. *lancifolia,* and 3) differentiation of all taxa from each other and their placement in subgeneric groups.

MATERIALS AND METHODS

Fifty-nine populations were measured from herbarium material for 58 characters (Table 2; data available from author). The number of populations sampled per taxon was based on 1) the amount of material available for each taxon, and 2) the amount of obvious variation present in each taxon. Quantitative characters were scored for each OTU (operational taxonomic unit, Sokal & Sneath, 1963; here a population) as the highest measure for that trait for each population sample. This was believed to be a better approach than using a mean or low number because it indicates the maximum genetic potential of each character. Following the populational computations, relationships among the individual taxa were determined using the average values for each taxon for the quantitative characters and the most common value for qualitative characters.

The techniques used in the analysis of these data were those contained in the NT-SYS package (Rohlf et al., 1972). Data were

Table 2. Characters and character states of *Tithonia* used in the numerical study. Numbers in parentheses indicate values for qualitative states or scale for quantitative measurements.

Habit and Stem. 1. Habit; herb (0), shrub (1), tree (2). **2.** Height (m). **3.** Stem pubescense: glabrous to sparse (0), moderate (1), dense (2).

Leaves. 4. Petiole length: sessile to 10 mm (0), 11–20 mm (1), 21 or greater (2). **5.** Leaf outline: linear (0), lanceloate (1), triangular (2), ovate (3), deltate (4), triangular or lanceolate and 3–5 lobed (5). **6.** Leaf base: cuneate (0), attenuate (1), attenuate-auriculate (2). **7.** Leaf color: above and below the same (0), above and below different (1). **8.** Leaf length (mm). **9.** Leaf width (mm). **10.** Leaf pubescence above: glabrous to sparse (0), moderate (1), woolly (2). **11.** Leaf pubescence below: glabrous to sparse (0), moderate (1), woolly (2).

Heads. 12. Nature of the peduncle: bract present (0), bract absent (1). **13.** Peduncle length (mm). **14.** Peduncle pubescence: glabrous to sparse (0), moderate (1), dense (2). **15.** Peduncle diameter (mm). **16.** Peduncle shape: constricted (0), even (1).

Phyllaries. 17. Total number of phyllaries. **18.** Number of phyllary series. **19.** Outer phyllary series length (mm). **20.** Outer phyllary series width (mm). **21.** Inner phyllary series length (mm). **22.** Inner phyllary series width (mm). **23.** Outer phyllary tip: round (0), pointed (1). **24.** Inner phyllary tip: round (0), pointed (1).

Ray florets. 25. Number of ray florets. **26.** Ray floret color: yellow (0), orange (1). **27.** Ray corolla length (mm). **28.** Ray corolla width (mm). **29.** Ray tube length (mm). **30.** Ray tube width (mm). **31.** Pappus present (0), absent (1).

Pales. 32. Pale length (mm). **33.** Pale tip length (mm). **34.** Pale width (mm). **35.** Pale texture: indurate (0), smooth (1). **36.** Vesture of pales: glabrous (0), pubescent on fold (1), pubescent on apical surface and fold (2), pubescent on edge (3). **37.** Pales enclosing achenes: loosely (0), tightly (1).

Disk florets. 38. Disk floret number. **39.** Disk throat length (above swollen base) (mm). **40.** Disk throat width (above swollen base) (mm). **41.** Disk tube length (mm). **42.** Disk tube width (mm). **43.** Base of throat length (mm). **44.** Base of throat width (mm). **45.** Disk lobe length (mm). **46.** Disk floret pubescence: base of throat (0), tube (1), base of throat and tube (2). **47.** Anther length (mm). **48.**

Anther color: black (0), brown or tan (1). **49.** Style branch length (mm). **50.** Style length (mm). **51.** Base of style: ovarian disk (0), swollen base (1), ovarian disk and swollen base (2).

Achenes (disk). **52.** Achene shape: rounded quadrangular (0), quadrangular (1), triangular (2). **53.** Achene color: black (0), brown (1), black or brown (2). **54.** Achene pubescence: absent (0), present (1). **55.** Achene length (mm). **56.** Achene width (mm). **57.** Pappus: none (0), squamellae (1), awns and squamellae (2).

Receptacle. 58. Diameter (mm).

standardized using the STAND subroutine resulting in a mean of zero and a standard deviation near unity. Correlation and distance matrices were computed using SIMINTVL. Cluster analyses were performed using the TAXON subroutine. Three techniques, single linkage, complete linkage, and unweighted pair group method using arithmetic averages (UPGMA), were used to evaluate both correlation and distance matrices. A cophenetic correlation coefficient was calculated following each clustering routine to determine the amount of distortion the phenogram showed relative to the relationships in the matrices. In addition to clustering, principal component analysis (PCA) was used to evaluate the data (Harmon, 1967). The subroutine FACTOR was used and both unrotated and rotated (Kaiser, 1958) (using VARIMAX) components were output. A minimum spanning tree was used with the PCA to detect distortion (Rohlf, 1970).

RESULTS AND DISCUSSION

Analysis of Populations. The similarities and differences of the genus have been summarized using two techniques: 1) cluster analysis, and 2) PCA. The cluster analysis technique which best summarizes the relationships between populations based on the highest cophenetic correlation coefficient (.86) is UPGMA (Fig. 7). The pairwise relationships of particular taxa were well illustrated. Populations of *Tithonia diversifolia* and *T. rotundifolia* formed clusters among themselves and were not grouped near each other (Fig. 7). They were, in fact, placed in different subgroups. The four populations (UK 1–4) from Honduras and Belize were also well resolved. These populations were grouped closely together but they tie in most closely to the populations of *T. longiradiata* (Fig. 7). Lastly, the similarity value between *T. auriculata* and *T. calva* var. *lancifolia* was quite high (Fig. 7). Two populations of *T. auriculata* clustered more closely with populations of *T. calva* var. *lancifolia* than with the third population of *T. auriculata*.

The cluster analysis also depicted the populational groups as well differentiated from one another (Fig. 7). Each taxon formed by a cluster of populations was grouped with another populational cluster at a much lower level. Most species pairs were grouped at the .35 level or lower. The pair representing *Tithonia longiradiata* and the unknowns (1–4) clustered at a slightly higher level (.39). These taxa represent morphologically more similar groups. At a somewhat lower level of clustering (−.19), the genus is divided into two subgroups of taxa. One group includes *T. calva* var. *calva*, *T. calva* var. *lancifolia*, *T. auriculata*, *T. longiradiata*, and the Honduras and Belize populations. The remaining taxa make up the second subgroup.

The PCA of these same populations resulted in the relationships depicted in Figure 8. In the first two principal components, which account for 37% of the variation, most of the population groups representing the same taxon are well differentiated (Fig. 8). The problem taxa, *Tithonia diversifolia* vs. *T. rotundifolia*, and *T. longiradiata* vs. UK 1–4, were as easily distinguished as they were in the cluster analysis. In addition, the *T. auriculata* populations and the *T. calva* var. *lancifolia* populations are close to each other. Adding the third component (9.7% of the variation) primarily separates the taxon *T. tubaeformis* from the others (Fig. 9). The rotated PCA resulted in essentially the same relationships in space and therefore are not presented. The PCA also clearly differentiated the two subgroups of taxa formed by the cluster analysis.

Analysis of Taxa. The analysis of the taxa gave somewhat different results concerning their pairwise similarities. The UPGMA technique again gave the highest cophenetic correlation coefficient (.87), but those taxa which were clustered most closely in the populational study were not those clustered together in this analysis (Fig. 10). Specifically, two taxa, *Tithonia fruticosa* and *T. pedunculata*, are those which differ in their relationships with other taxa. *Tithonia pedunculata* is most closely clustered with *T. tubaeformis*, and *T. fruticosa* with the group including *T. calva* (+ 2 vars.), *T. auricu-*

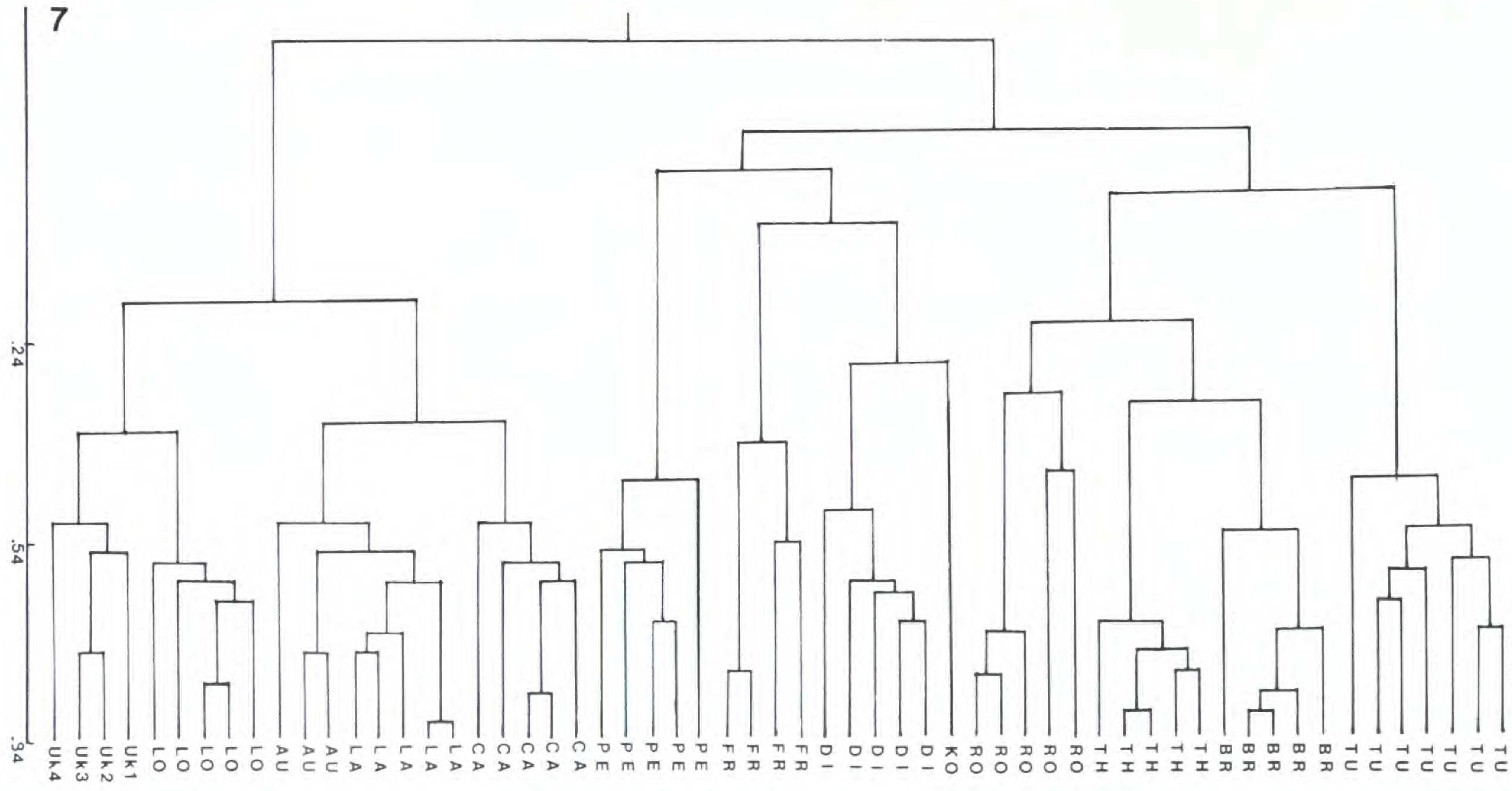
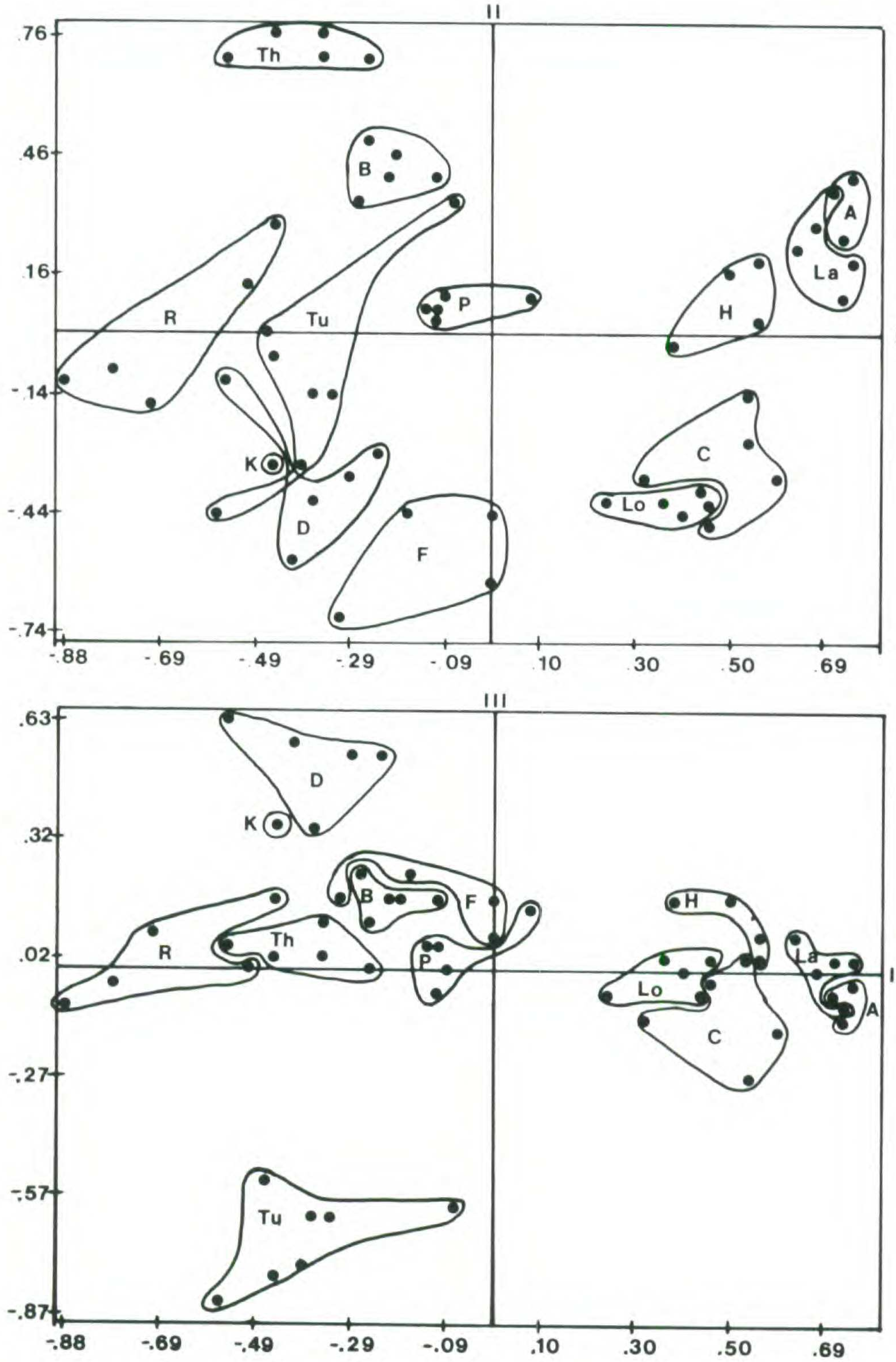


Figure 7. Phenogram of population of *Tithonia* using UPGMA. Taxa are abbreviated using the first two letters of the specific or varietal epithet (see Table 4). Uk 1–4 are populations from Belize and Honduras of uncertain affinity. Scale is the level of correlation.



Figures **8 & 9.** First three principal component axes from analyzing populations of *Tithonia* (unrotated); **8,** first and second principal component axes; **9,** first and third principal component axes.

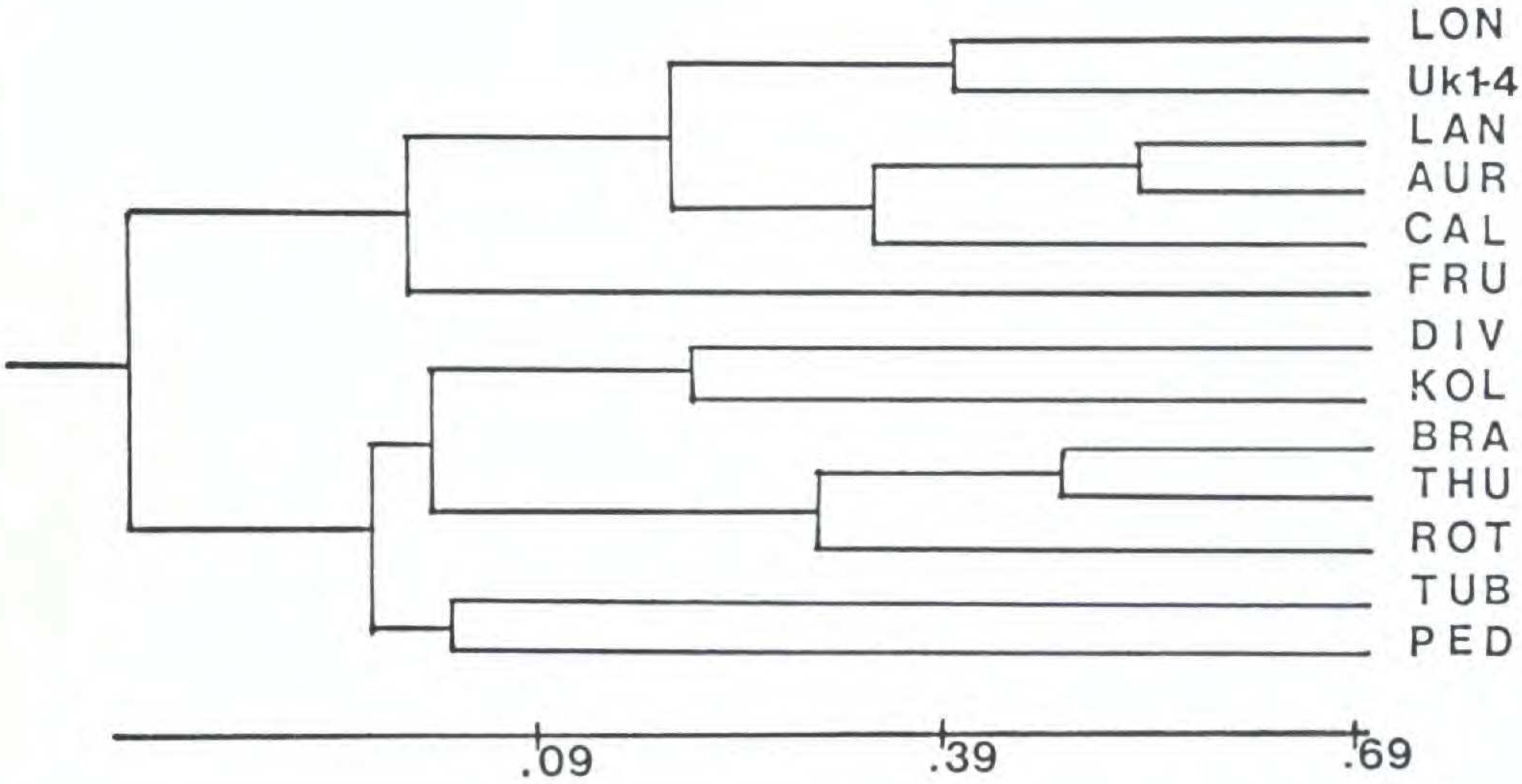


Figure **10**. Cluster analysis (UPGMA) of summarized data for taxa of *Tithonia*. Scale is level of correlation.

lata, UK 1–4, and *T. longiradiata*. The level of clustering was very low in both cases (less than .09) indicating that these are not strongly similar taxa, but are instead placed here based on very few similarities. These distortions may occur due to the summarization of the data by averaging the values for quantitative characters and taking the most common state for qualitative characters. This summarization of data for each taxon reduces the variation present in each taxon, and the similarities and differences are distorted.

The PCA results were quite similar to those obtained in the cluster analysis (Fig. 11). Three-dimensional PCA is sometimes difficult to interpret, because it is known to distort close relationships (Rohlf, 1970). The MST helps reveal these areas of distortion. For instance, *Tithonia calva* (+ 2 vars.), *T. auriculata, T. longiradiata*, and UK 1–4 on the plot of the first three principal components appear close to each other and the MST supports these relationships. The relationship of *T. fruticosa* with *T. koelzii*, as shown by the MST, is similar to that in cluster analysis (Fig. 7). Again, the relationships of *T. pedunculata* with an annual taxon, in this case *T. thurberi*, is not consistent with any of the previous analyses. An additonal relationship which is evident from this analysis, as well as the cluster analysis and PCA of populations, is that two main groups of taxa are formed: one group including *T. calva* (+ 2 vars.), *T. longiradiata, T. auriculata*, and the Honduras and Belize populations; and the second group the remaining taxa.

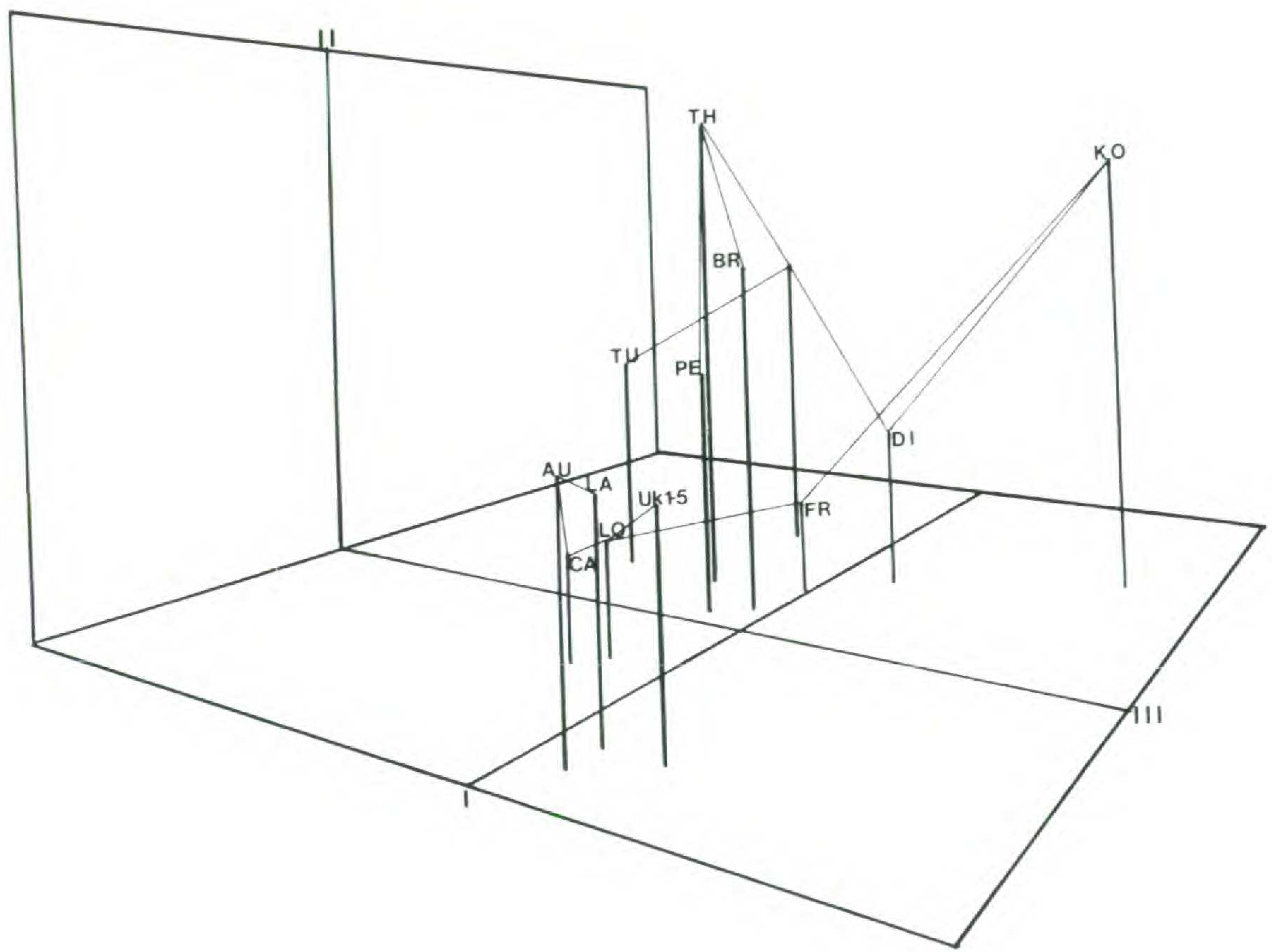


Figure **11.** Principal component analysis (unrotated) in three dimensions of data for taxa of *Tithonia.* Minimum spanning tree is overlain.

CONCLUSIONS

A number of patterns of variation can be resolved from these anlayses. First, the populations of *T. longiradiata* from Honduras and Belize should be recognized at the rank of species. This taxon has already been described elsewhere as *T. hondurensis* La Duke (La Duke, 1982) to prevent a *nomen nudum* from occurring in a paper published prior to this revision. These populations are grouped together consistently and possess a set of characters which differentiate them at a level warranting the rank of species. Second, the two taxa, *T. diversifolia* and *T. rotundifolia*, can be consistently differentiated from one another and should be retained at the rank of species. Third, the taxon *T. auriculata* should be given the rank of variety under *T. calva* (called *T. calva* var. *auriculata;* see taxonomic section). The characters which differentiate it from its closest relative, *T. calva* var. *lancifolia* are minor and the level of clustering supports this similarity. Fourth, two subgroups can be delimited within the genus as follows: 1) *T. calva* (and its 3 vars.), *T. hondurensis*, and *T. longiradiata;* and 2) the remaining eight taxa. These patterns of variation suggest that two subgeneric taxa should be recognized.

PHYLOGENETIC RECONSTRUCTION

The development of phylogenetic hypotheses has been part of botanical revisionary studies for many years (e.g. Canne, 1977; Stuessy, 1978). However, the documentation of methods and interpretation of the resultant phylogenetic diagrams have not always been adequate (Funk & Stuessy, 1978). Three steps are important in phylogenetic reconstruction: 1) the choice of units to use in the evolutionary analysis, 2) the selection of characters and states, and their polarity, and 3) the choice of a method to evaluate these data. Superficially, these steps seem straightforward, but controversy exists concerning the theory behind each.

The choice of evolutionary units is the first step in phylogenetic reconstruction, and it depends on the questions being asked. In the case of *Tithonia*, the interest is in the evolutionary relationships among the taxa. Consequently, the taxa become the evolutionary units.

The choice of characters, states, and the determination of polarity is more difficult. Characters and character states are usually easily determined for qualitative characters and somewhat more difficultly for quantitative characters since discrete character states are not usually evident. The characters are not useful, however, unless the evolutionary polarity for each can be hypothesized. The different methods of determining character polarity have been recently reviewed (Crisci and Stuessy, 1980; Watrous & Wheeler, 1981). Many of the methods which have been proposed are not applicable to *Tithonia* (i.e., fossils), or have a low confidence level (i.e., ingroup common equals primitive). One effective method for polarity determination is the related-group (or outgroup) criterion (Kluge & Farris, 1969; Lundberg, 1972). Related-group comparison has the following assumptions. First, the most closely related taxon or group of taxa to the one in question can be estimated. In the case of *Tithonia*, the outgroup consists of members of *Viguiera* subgenus *Amphilepis* and subgenus *Calanticaria*. Second, a character state which is shared by the outgroup and the taxon being investigated is regarded as ancestral. Since the two groups shared a common ancestor most recently, it is logical that any changes from the primitive form will show in one of the two ancestors. This technique was used in character polarity determination.

The last step, choice of method, is also somewhat controversial. The basis for many of the methods of phylogeny reconstruction. stem from Hennig (1950, 1966). Hennig detailed a theoretical basis for phylogenetic reconstruction, and applied these to specific organisms. Expansion of these ideas and possibly more importantly, the advancement of new ideas of phylogeny reconstruction has led to numerous techniques for evaluation of evolutionary data. These techniques include: Prim networks (Prim, 1957), the Weighted Invariant Step Strategy, WISS (Farris et al., 1970), the clique, or character compatibility method (LeQuense, 1969, 1972; Estabrook et al., 1975, 1976a, b), and Wagner methods (Kluge & Farris, 1969; Farris, 1970). Considerable literature exists concerning the validity of each of these techniques (for review see Funk & Stuessy, 1978; Farris & Kluge, 1979), and two main schools predominate: 1) character compatibility, and 2) parsimony. Character compatibility removes those characters which show reversals or parallelisms, and may result in incomplete resolution of small groups of taxa. The technique does not make estimates of the best fit for parallelisms or reversals in character trends, but instead leaves those judgments for the biologist studying the group. The parsimony technique minimizes the parallelisms and reversals to produce a more resolved diagram of the relationships. For this reason, a representative technique from each group has been utilized in this study; the character compatibility technique of Estabrook et al. (1975, 1976a, b); and the parsimony technique of Farris (1970) (Wagner 78 version).

The purpose of these analyses is to: 1) develop hypotheses as to character trends in *Tithonia*, 2) utilize character compatibility and parsimony to evaluate the phylogenetic relationships, and 3) compare these results with the relationships determined by the numerical taxonomic techniques to help produce an even more predictive classification.

MATERIALS AND METHODS

The characters which were initially evaluated were those used in the numerical taxonomic study. Most of the quantitative characters were not used because accurate discontinuities could not be detected in the data which could be evaluated evolutionarily. No character states which were unique to only one taxon were used because they do not give information about the between-taxa relationships; they only reinforce the unique nature of the species. The outgroup used for determining the polarity of the character trends were taxa from the subgenera *Amphilepis* and *Calanticaria* of *Viguiera*. These taxa were chosen because, within *Viguiera*, they form the most closely related group to *Tithonia*. Fourteen characters finally were selected for use in the analyses (Table 3).

The determination of two of these characters is somewhat difficult and a brief explanation is in order. There are two types of leaf attachments, sessile and petiolate, in *Tithonia*, sessile being advanced. The leaf bases on these leaves are either auriculate or not, but the auriculae are not of the same nature on sessile and petiolate leaves. In the former, they are persistent, and in the latter, they are ephemeral (in the sense that the auriculae may not always be produced on each leaf, and if produced, may rapidly dry and brown). The nature of the pappus is the second difficult character set. Achenes in *Tithonia* are of three types (Fig. 2–4): epappose, a pappus of fused squamellae, or a pappus of squamellae plus two awns. The outgroup has squamellae plus awns (Fig. 1). I view these characters in the following way: one character is the presence or absence

Table 3. Characters and character states used in the phylogenetic reconstruction of *Tithonia*.

Character	Character State	
	Ancestral (A)	Derived (D)
1. Duration	perennial	annual
2. Leaf attachment	sessile	petiolate
3. Persistent auriculae of leaf base	absent	present
4. Ephemeral auriculae of leaf base	absent	present
5. Leaf shape	linear to deltate	3-5 lobed
6. Nature of the peduncle	unconstricted	constricted
7. Ray ligule length	short	long
8. Number of series of phyllaries	2-3	4
9. Pale length	short	long
10. Anther color	black	brown
11. Achene shape	triangular or quadrangular	rounded quadrangular
12. Achene vesture	pubescent	glabrous
13. Pappus	present	absent
14. Nature of Pappus	with awns or absent	only fused squamellae

of pappus, with the absence being derived, and the other character is the specialized nature of the pappus in the taxa with fused squamellae, but lacking awns. I view this as a derived character state independent of the loss of pappus. It may be argued that the four characters of leaves and pappus might better be regarded as transformational series of only two characters. An hypothesis for the leaf transformation would begin with the petiolate condition as primitive, the petiolate plus auriculate condition as derived in one direction and the sessile condition in the other. The sessile, auriculate condition is then further derived from the sessile condition. Similarly, one might hypothesize that the pappus transformation has gone from achenes with squamellae plus awns as primitive, and the epappose and squamellar conditions as derived in opposite directions from it. To evaluate these possibilities, these trends were also employed in the analysis. The data matrix of the fourteen characters is presented in Table 4 (showing the first leaf and pappus trends only). Both character compatibility and Wagner 78 were used to evaluate these data.

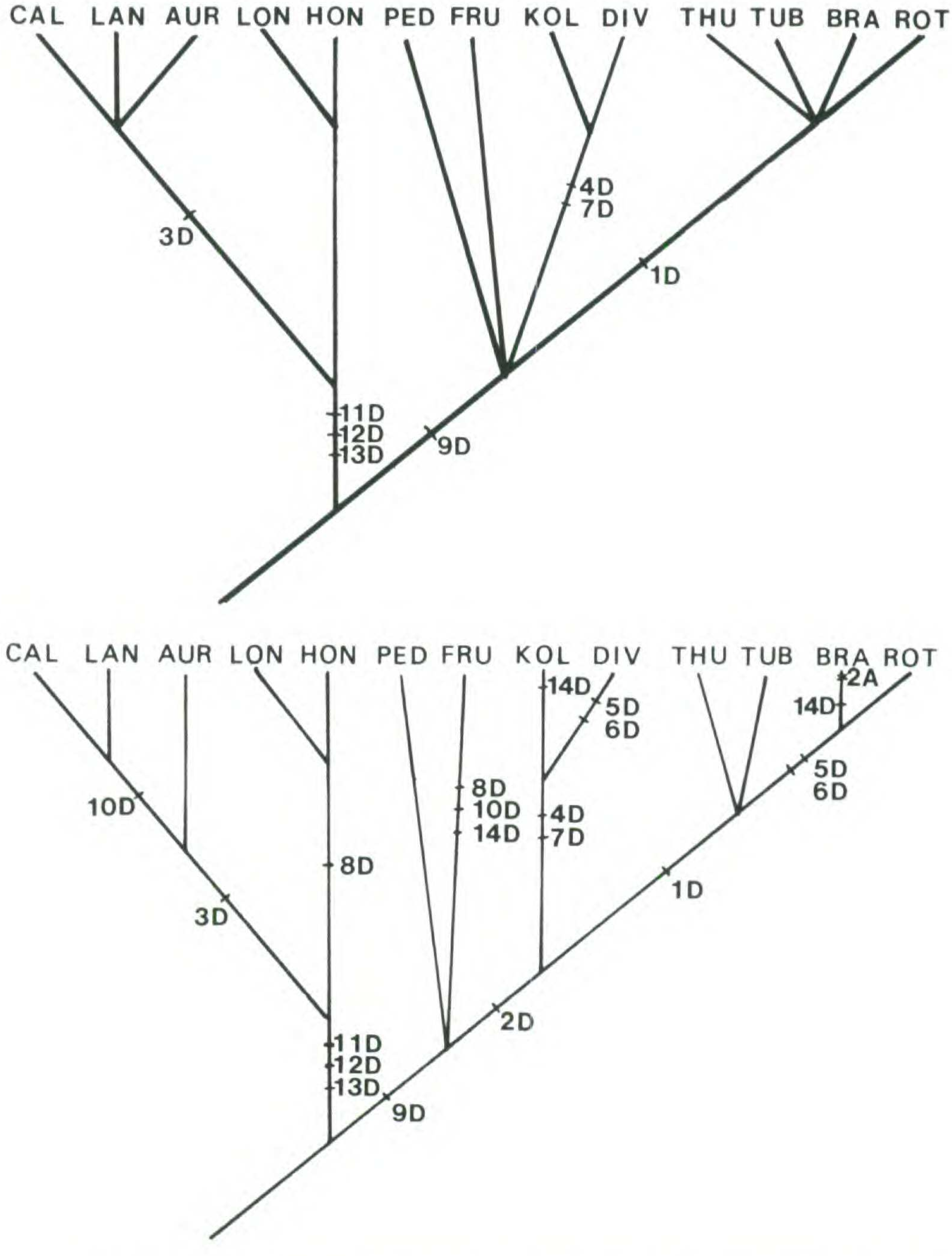
Table 4. Data matrix for the phylogenetic reconstruction of *Tithonia*. 0 = ancestral, 1 = derived.

Taxon	Characters													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
T. brachypappa	1	1	0	0	1	1	0	0	1	0	0	0	0	1
T. calva var. *auriculata*	0	1	1	0	0	0	0	0	0	0	1	1	1	0
T. calva var. *calva*	0	1	1	0	0	0	0	0	0	1	1	1	1	0
T. calva var. *lancifolia*	0	1	1	0	0	0	0	0	0	1	1	1	1	0
T. diversifolia	0	0	0	1	1	1	1	1	1	0	0	0	0	0
T. fruticosa	0	1	0	0	0	0	0	1	1	1	0	0	0	1
T. hondurensis	0	1	0	0	0	0	0	1	0	0	1	1	1	0
T. koelzii	0	0	0	1	0	0	1	0	1	0	0	0	0	1
T. longiradiata	0	1	0	0	0	0	0	1	0	0	1	1	1	0
T. pedunculata	0	1	0	0	0	0	0	0	1	0	0	0	0	0
T. rotundifolia	1	0	0	0	1	1	0	0	1	0	0	0	0	0
T. thurberi	1	0	0	0	0	0	0	0	1	0	0	0	0	0
T. tubaeformis	1	0	0	0	0	0	0	0	1	0	0	0	0	0

RESULTS AND DISCUSSION

The character compatibility technique produced two trees, both using eight of the 14 characters. Both diagrams used the following seven characters: 3, 4, 7, 9, 11, 12, and 13. Character 1 was used in organizing one tree (Fig. 12) while character 2 was used in the other. Since both of the trees used the same number of characters with only one difference between them, each tree is judged equally acceptable. One of these trees (Fig. 12) was, however, chosen for comparison with the diagram produced by the parsimony technique (Fig. 13) because of their similarity.

The parsimony technique has a higher level of resolution (Fig. 13). In this technique, all the characters are utilized in constructing the phylogenetic diagram. Five characters exhibit parallel evolution in this group based on the most parsimonious arrangement of the



Figures **12 & 13.** Cladograms of taxa of *Tithonia* based on character compatibility (**12**) and Wagner 78 (**13**) analyses. Changes in characters on the tree from the ancestral to the derived (D) state are indicated by number (See Tables 3 and 4). Refer to Table 4 for complete names of taxa. One reversal occurs in character 2(A) in Fig. 13 (double bar).

characters. The derived character states for these characters are: 3–5 lobed leaved (5D), constricted peduncle (6D), 4 phyllary series (8D), brown anthers (10D), and pappus of fused squamellae (14D). The parallel nature of each of these states can be traced in Fig. 13. Only one character shows a reversal and that is the nature of the leaf attachment (2). Petiolate leaves is the derived state of this character and serves to unite seven of the basal taxa, but the taxa forming the group *Tithonia diversifolia, T. koelzii, T. rotundifolia,* and *T. tubaeformis* all have petiolate leaves. Since the primitive condition is sessile the trend reverses with *T. brachypappa.*

Utilizing the alternate character trends for the nature of the pappus and leaf attachment, the results are more complex than those already presented for both techniques. The character compatibility program used only five of the now twelve characters resulting in larger unresolved clusters of taxa. The parsimony technique produced a diagram with a greater number of necessary character changes and increased the amount of parallelism and reversal in the tree.

A number of evolutionary groups are evident from these analyses. First, two main groups diverged early. One group includes the three taxa, *Tithonia calva* (+ 3 vars.), *T. hondurensis,* and *T. longiradiata.* This group shares a number of important achene character states (11, 12, 13). The other group of the remaining taxa is united based on the nature of the pales. This group can be further subdivided into three evolutionary lines. One line includes the two taxa *T. fruticosa* and *T. pedunculata.* These are united with this large group based on the nature of the pales, but do not share derived states of other characters with individual members of the group. Therefore, the position of these two taxa early in the evolution of the line is required. Using numerical techniques, these two taxa are quite similar, but they are problem taxa even with these methods. Given new data, the resolution of this multiple branch on the diagram may be possible.

Tithonia diversifolia and *T. koelzii* form a second group. These taxa are united based on two unique character states. One is the nature of the auriculae. Logically, the evolution of this unusual character state on two separate lines is not as probable as its occurrence in the ancestor of two closely related taxa. These two taxa also share the trait of longest ray florets in the genus.

The last group has the advanced trait of all being annuals. These four taxa are quite similar morphologically and the monophyletic origin of the annual habit would support these similarities. *Tithonia thurberi* and *T. rotundifolia* are further differentiated based on the nature of the peduncle and leaf margin.

These four groupings correspond well not only to the data derived from the evolutionary analyses, but also to the data resulting from the numerical taxonomic studies. Referring to Fig. 7, it is immediately evident that the two main groups formed in the phylogenetic reconstruction are the two main clusters formed in the numerical taxonomic analysis. Further, the subgroups are also supported. Only in the case of the relationships of *T. pedunculata* and *T. fruticosa* is there a discrepancy. The clustering level, however, is very low and not as powerful as their grouping based on an evolutionarily determined character trend. Based on the numerical taxonomic study and the phylogenetic reconstruction, the taxa within the subgeneric categories (La Duke, 1982) are (see Taxonomic Treatment for validation): Section *Tithonia:* Series *Tithonia (T. rotundifolia, T. tubaeformis, T. thurberi, T. brachypappa);* Series *Grandiflorae (T. diversifolia, T. koelzii);* Series *Fruticosae (T. fruticosa, T. pedunculata):* Section *Mirasolia (T. calva* [+ 2 vars.], *T. hondurensis, T. longiradiata).*

MORPHOLOGY AND TAXONOMIC CRITERIA

As a guide to the use of the keys and descriptions in *Tithonia,* details of the taxonomic value of morphological characters in the genus are given below.

Habit. Two basic types of habit appear within *Tithonia.* The first is herbaceous, with ascending stems in *T. brachypappa, T. rotundifolia, T. thurberi,* and *T. tubaeformis.* The second is the woody condition in the remainder of the genus. Variation occurs from weakly woody in *T. diversifolia, T. fruticosa,* and *T. koelzii,* to strongly woody shrubs such as *T. calva* and *T. pedunculata.*

Leaves. Leaf shape, base, and the presence or absence of a petiole are reliable characters in recognition of taxa. The most common leaf shape is linear-lanceolate, but variation ranges from linear in *Tithonia calva* var. *auriculata* to deltate in *T. tubaeformis* to 3–5 lobed in *T. diversifolia* and *T. rotundifolia.* Most taxa have sessile leaves, but four taxa are always petiolate: *T. koelzii, T. rotundifolia, T. thur-*

beri, and *T. tubaeformis*. Winged petioles are absent in *Tithonia*, but long leaf bases are present resulting in many sessile leaves. Leaf bases are either attenuate, auriculate, or decurrent. *Tithonia koelzii* and *T. diversifolia* have an unusual auricle at the base of the petiole. This condition is found in these species only when grown in mesic conditions, but the adaptive value is unknown.

Involucre. The phyllaries comprising the involucres are of two types. The spathulate type is the most common, with the linear or oblong type found in six taxa. The number of series of phyllaries ranges from 2 to 4 (5) and can be used in many taxa as a reliable character. In some taxa (e.g. *T. longiradiata*), the innermost series of phyllaries approaches the nature of pales. They are tan, striate, and have the characteristic paleaceous acuminate tip. In some taxa, the overall nature of the phyllaries is the best character for species recognition, but it is difficult to describe effectively.

Pales. The pales of taxa of *Tithonia* sort neatly into two types. Aristate-tipped loosely enclosing pales occur in Section *Tithonia*. In contrast, shorter, acute to infrequently aristate pales which tend to enclose the achenes tightly occur in section *Mirasolia*.

Florets. Few floret characters are useful in differentiating taxa. Most populations of *Tithonia rotundifolia* have orange ray florets, but the yellow condition typical of the other taxa of *Tithonia* also occurs in some populations. Anther color is black in the disk florets in most taxa except *T. calva* and *T. fruticosa*, which have tan or brown anthers. The shape of the disk floret varies very little and is not useful in delimiting taxa. Anther length is useful in recognizing some taxa, such as *T. calva* var. *calva* vs. *T. calva* var. *lancifolia*, but it varies considerably in others.

Achenes and Pappus. Shape of the achenes and nature of the pappus are important at the sectional and in some cases at the specific levels. Section *Mirasolia* is characterized by small (3–5 mm) rounded-quadrangular, black or mottled epappose achenes with eliasomes. Section *Tithonia* is characterized by larger (4.5–9 mm) quadrangular or triangular, black, brown, or mottled pappose achenes. The pappus is a basally and laterally fused squamellar ring with or without awns (Figs. 2 & 3). One taxon of this section, *T. pedunculata*, has, in addition to pappus, an eliasome at the base of the achene.

TAXONOMIC TREATMENT

Tithonia Desf. ex Juss.

Tithonia Desf. ex Juss. Gen. Pl. 189. 1789.

Tithonia Desf. ex Gmelin, Syst. Nat. **2:** 1259. 1791.
TYPE species: *Tithonia uniflora* Desf. ex Gmelin = *Tithonia rotundifolia* (Mill.) S. F. Blake.
Tithonia subgen. *Mirasolia* Sch.-Bip. in Seemann, Bot. Voyage Herald **305.** 1856. TYPE species: *Tithonia calva* Sch.-Bip in Seemann.
Mirasolia (Sch.-Bip. in Seemann) B. & H. Gen. Pl. **2:** 367. 1873.
Urbanisol O. Kuntze, Rev. Gen. Pl. **1:** 370. 1891.
Superfluous name, based on type of *Tithonia* Desf. ex Gmelin.

Erect, annual or perennial, herbs, shrubs, or trees. Stems terete, yellow, green, brown, or purple; glabrous to densely villous with hairs to 15 mm long. Leaves alternate (occasionally opposite below), petiolate or sessile; blades linear to deltate or 3–5 lobed, at apex acute to acuminate, at base attenuate to auriculate or decurrent, on upper surface pilose to subglabrous, on lower surface pilose to subglabrous, at margin serrate to crenate. Peduncle hollow-flared (fistulose), villous to pilose or subglabrous. Heads mostly solitary. Receptacle hemispheric to convex; pales stiff, striate, aristate to acuminate or acute, usually with two secondary lobes, embracing the achenes, persistent. Phyllaries 2–5 seriate, graduated, linear to broadly rounded, at apex acute to rounded, glabrous to pilose. Ray florets 8 to 30, neuter; ligules yellow or orange, pappus present or absent; achenes white to light tan, triangular. Disk florets hermaphrodite; corollas yellow, with lobes 5; anthers black, brown, or tan; styles bifid, at base usually swollen, with or without an ovarian disk[1]; stigmas pappillate; pappus absent or of fused squamellae and sometimes awns; achenes fertile, black, brown, or mottled, triangular, rounded-quadrangular to quadrangular; with or without eliasome at base. Chromosome number, $n = 17$. TYPE SPECIES: *Tithonia uniflora* Desf. ex Gmelin = *Tithonia rotundifolia* (Mill.) S. F. Blake.

KEY TO THE TAXA

1. Achenes of the disk florets all epappose .... (2)
   2. Phyllaries linear to lanceolate, acute-tipped .... (3)

[1]The structure encircles the style at the base on top of the ovary. It is probably a nectary, but it is not known if nectar is produced.

3. Leaves linear to linear-lanceolate, usually with one main vein, 8–12 times as long as broad .... 9c. *T. calva* var. *auriculata*
3. Leaves ovate to lanceolate-ovate (sometimes linear-lanceolate) with main vein branching into three smaller veins about 1/3 of the way up from the base, less than 8 times as long as broad .... (4)
4. Heads 7–9 mm diam; outer phyllaries 7–9 mm long; anthers 1.5–2 mm long............. 9b. *T. calva* var. *lancifolia*
4. Heads 10–14 mm diam; outer phyllaries 10–14 mm long; anthers 3.5 mm long ....9a. *T. calva* var. *calva*
2. Phyllaries oblong with broadened tips................................ (5)
5. Leaves linear to linear-lanceolate with margin revolute, 0.5–2.8 cm wide; disk florets about 60–80 .. 11. *T. hondurensis*
5. Leaves triangular to ovate to long-lanceolate, without strongly revolute margin, 2.6–13.5 cm wide; disk florets about 100–200 .... 10. *T. longiradiata*
1. Achenes of at least some of the disk florets with pappus........ (6)
6. Leaves lanceolate to lanceolate-ovate, at margin entire to crenate .... (7)
. Phyllaries 3-seriate, linear; leaves hispid; occurring only in Oaxaca, Mexico ....8. *T. pedunculata*
7. Phyllaries 4-seriate, ovate; leaves soft-villous; occurring in northern Mexico..................................... 7. *T. fruticosa*
6. Leaves deltate, at margin entire to 3–5 lobed...................... (8)
8. Leaf base strongly decurrent on stem..... 2. *T. brachypappa*
8. Leaf base attenuate or with only ephemeral auriculate lobes at base of petiole.. (9)
9. Phyllaries in 2 series.............................3. *T. tubaeformis*
9. Phyllaries in 3–4 series ....(10)
10. Ligules of ray florets greater than 45 mm long......(11)
11. Large shrub; leaves deltate and/or 3–5 lobed; phyllaries 4- (rarely 3-) seriate; widespread in Mexico and Central America; disk florets 80–120 .... 6. *T. diversifolia*
11. Small tree; leaves all deltate; phyllaries 3-seriate; endemic to Jalisco; disk florets 60 or less................ .... 5. *T. koelzii*
10. Ligules of ray florets less than 33 mm long ....(12)
12. Ray florets orange (rarely yellow); ligules 20–33 mm

long, 6–17 mm wide; leaves deltate and/or 3–5 lobed, soft-pubescent, anthers 4–5.5 mm long......... ....1. *T. rotundifolia*

12. Ray florets yellow; ligules 9–15 mm long, 4–6 mm wide; leaves deltate, hispid; anthers 2–4 mm long... ....4. *T. thurberi*

I. *Tithonia* section *Tithonia*

Tithonia Desf. ex Juss. Gen. Pl. 189. 1789. TYPE SPECIES: *Tithonia uniflora* Gmelin = *Tithonia rotundifolia* (Mill.) S. F. Blake.

Shrubs or herbs; leaves lanceolate to deltate, sessile to petiolate, with margin serrate to 3–5 lobed; involucre 2–5 seriate; disk achenes quadrangular or triangular, pubescent, with pappus of fused squamellae, with or without awns, or nearly lacking in some achenes. Species 1–8.

1. Series *Tithonia*

Herbaceous annuals; leaves deltate to 3–5 lobed; involucre 2–3 seriate. Species 1–4. TYPE SPECIES: *Tithonia rotundifolia* (Mill.) S. F. Blake.

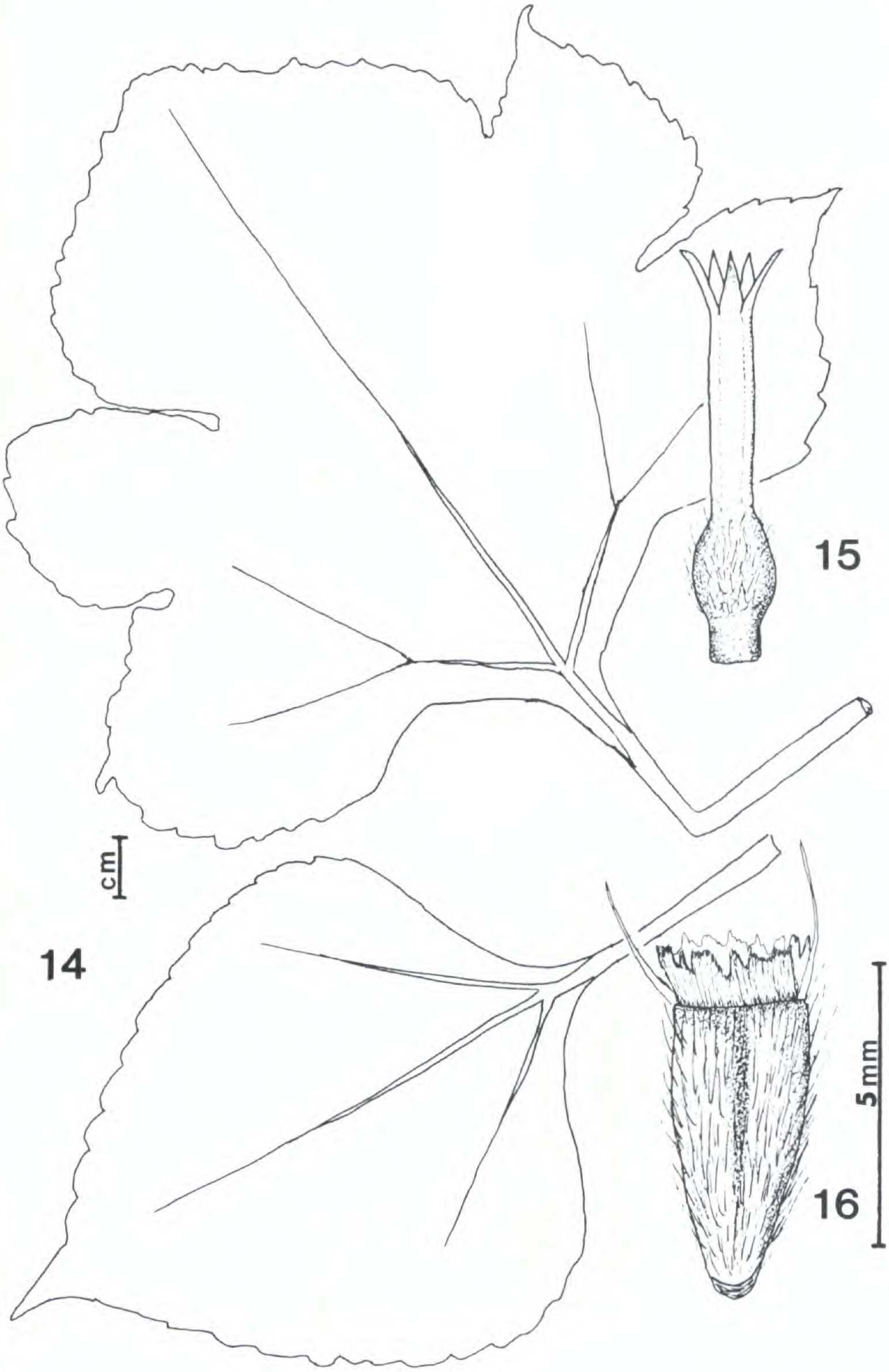
1. **Tithonia rotundifolia** (Miller) S. F. Blake, Contr. Gray Herb. ser. **52:** 41. 1917 Figs. 14–16.

Tagetes rotundifolia Miller, Gard. Dict. ed. **8.** *Tagetes* #4. 1768. TYPE: MEXICO, Veracruz, grown from seed, probably at the Chelsea garden, *W. Houstoun s.n.* (HOLOTYPE, BM! [photo, GH!, NY!, OS!, UC!]).

Tithonia uniflora Desf ex Gmelin, Syst. Nat. ed. 1791, *t.2.* 1259. 1791. TYPE: location, date, and collector unknown. (HOLOTYPE, not located). The location of J. F. Gmelin's herbarium is unknown (Stafleu & Cowan, 1976).

Tithonia tagetiflora Lamarck, Tabl. Ency. Metd. **2:** 284, *t. 708.* 1797. TYPE: location, date and collector unknown (HOLOTYPE, the illustration is taken as the type). Although J. B. Lamarck's herbarium is housed at Paris (P-LA), no specimen has been located.

Tithonia tagetiflora Desf. Ann. Mus. Natl. Hist. **1:** 49. *pl. 4.* 1802. TYPE: specific locality unknown, date unknown, *Thiery s.n.* (HOLOTYPE, P [photo GFND!, OS!]).



Figures **14–16.** Leaf outlines (Fig. **14**; *La Duke et al. 510a,* OS), disk corolla (Fig. **15**), disk achene (Fig. **16**) of *Tithonia rotundifolia.* Figures 15 and 16, *La Duke et al. 480,* OS; same scale.

Helianthus speciosus Hook. Curtis Bot. Mag. ser. 2. **3:** *t. 3295.* 1834. TYPE: location, date and collector unknown (HOLOTYPE, K! [photo, GH!, NA!, OS!]).

Leighia? speciosa (Hook.) DC. Prodr. 5: 583. 1836.

Tithonia aristata Örsted, Natur. For. Kjob. Vid. Medd. **1852:** 114. 1852. TYPE: COSTA RICA, Aguacate, No date *A. S. Örsted s.n.* (HOLOTYPE, specimen not found, drawings of presumed holotype at C!). The handwriting on the drawing at C is that of Örsted and the drawing matches well with the description.

Tithonia heterophylla Griseb. Bonplandia **6:** 9. 1858. TYPE: PANAMA, specific locality unknown, 1810, *E. P. Duchassaing s.n.* (HOLOTYPE, GOET! [photo, OS!]; ISOTYPE, GOET! [photo, OS!]).

Tithonia speciosa (Hook.) Griseb. Cat. Pl. Cub. 155. 1866.

Tithonia macrophylla S. Wats. Proc. Amer. Acad. Arts. **26:** 140. 1891. TYPE: MEXICO. Jalisco, Barranca near Guadalajara, Sept 1889, C. G. *Pringle 2798* (HOLOTYPE, US!; ISOTYPES, F!, GH!, MICH!, NY!, US!).

Urbanisol tagetfolius var. *normalis* O. Kuntze, Rev. Gen. Pl. **1:** 370. 1891. TYPE: Location, date, and collector unknown (HOLOTYPE, not located).

Urbanisol tagetifolius var. *speciosus* O. Kuntze, Rev. Gen. Pl. **1:** 370. 1891. TYPE: location, date, and collector unknown (Holotype, not located).

Urbanisol aristatus (Örsted) O. Kuntze, Rev. Gen. Pl. **1:** 371. 1891.

Urbanisol heterophyllus (Griseb.) O. Kuntze, Rev. Gen. Pl. **1:** 371. 1891.

Tithonia speciosa (Hook.) Klatt in Durand & Pittier, Ext. Bull. Soc. Roy. Bot. Belg. **31:** 203. 1893. Invalid name, later homonym.

Tithonia vilmoriniana Pampanini, Bull. Soc. Bot. Ital. **1908:** 133. 1908. TYPE: MEXICO, Michoacan, Jacona, *Collector unknown s.n.* (HOLOTYPE, FI!).

Erect, annual, herbaceous, 1–4 m tall. Stems round, green to tan to purple, glabrous to softly pubescent. Leaves alternate with petioles 2–10 cm long; blades deltate to triangular to 3–5 lobed, 9–38 cm long, 4–30 cm wide, at apex acute to acuminate, at base attenuate, on upper surface glabrous to hispid, on lower surface sparsely pubescent to villous, at margin crenate to serrate. Peduncles 11–27 cm long, 3–10 mm diam, short-villous to to glabrous near head. Heads usually solitary, heterogamous. Receptacle 7–13 mm diam. Phyllaries 14–21, (two) three-seriate, graduated, linear to lanceolate; outer bracts 17–30 mm long, 4–7.5 mm wide, at apex acute, dense minute pubescence on abaxial surface; inner bracts 16–28 mm long, 5–8 mm wide, at apex acute to rounded, dense minute pubescence on abaxial surface. Pales striate, 11.5–15 mm long, 2–3 mm wide, apex acuminate to aristate, 2.5–5.5 mm long, usually with secondary lobes, occasionally minutely pubescent on tip. Ray florets 8–13; ligules usually orange, sometimes yellow, oval to oblong, 20–33 mm long, 6–17 mm wide, at apex trifid; tube 1.5–2.5 mm long, 0.75–1 mm diam, pappus absent or short scales or awns; achenes one-seriate, triangular, white-tan, sterile. Disk florets about 60–90; corollas yellow; corolla lobes 5, 1 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 3.5–5 mm long, 1–1.5 mm diam, with expanded portion 1–2 mm long, 1–2 mm diam; tube minutely pubescent, 0.5–1.25 mm long, 0.5–1 mm diam; anthers black, 4–5.5 mm long; styles 7–10 mm long; stigmas pappillate, 2–3.5 mm long; pappus fused squamellae with 2 awns; achenes fertile, quadrangular, black, brown, or mottled, pubescent, 5–7 mm long, 1.5–2.5 mm diam, at base smooth without eliasome. Chromosome number $n = 17$.

PRINCIPAL FLOWERING TIME: November — January.

DISTRIBUTION: Tropical forests or open areas throughout central and southern Mexico, south to Panama (Fig. 17). Introduced worldwide and escaped.

Tithonia rotundifolia is the type species of the genus. The plants are widespread throughout most of Mexico and Central America. Populations with orange rays are typical but yellow-rayed populations exist *(La Duke et al. 520 & 529),* mostly in Central America.

This taxon has been often confused with *Tithonia diversifolia,* from which it differs in many features. *Tithonia rotundifolia* is an annual, with linear-lanceolate phyllaries in (two-) three series and ray ligules 20–33 mm long, whereas *T. diversifolia* is a herbaceous perennial, with lanceolate to broadly ovate phyllaries in (three-) four series, and ray ligules 48–69 mm long. These taxa often are confused due to the similarity of the 3–5 lobed leaves. Recently the embryology of this taxon was described (Pullaiah, 1978) but no comparisons with other taxa of *Tithonia* were included.

REPRESENTATIVE SPECIMENS. ARGENTINA. **Jujuy:** Huaico, *Cabrera et al. 23594* (F). BELIZE. **Cayo:** El Cayo, *Bartlett 12099* (F, GH, LL, MICH, NA, US). CHINA. **Kiangsu:** Nanking, *Chiao 12955* (C, UC). COSTA RICA. **Alajuela:** 5–10 mi W of Naranjo on rte ca-1, *Stuessy & Gardner 4452* (OS); on freeway near Grecia, *Stuessy & Gardner 4468* (OS); ca 15 mi S of La Marina, then to Balneario Agua Caliente, *Stuessy & Gardner 4467* (OS). **Puntarenas:** 35.1 mi SE of San Isidro del General on rte 2 (ca-1), *Stuessy & Gardner 4505* (OS). CUBA. **Havana:** Vento, *Wilson 1325* (F, GH, NY, POM, US). EL SALVADOR. **Ahuachapán:** 5 mi SE of Hachadura (Guatemala border) on rte ca-2, *Stuessy & Gardner* 4565 (OS). **La Libertad:** ca 13 mi W of La Libertad on rte ca-2, *Stuessy & Gardner 4564**[1] (OS). **San Miguél:** 24.3 mi E of El Transito on rte ca-2. *Stuessy & Gardner* 4562 (OS). **Sonsonate:** vicinity of Izalco, *Pittier 1976* (F, US). GUATEMALA. **Chiquimula:** just W of town of Concepción Las Minas, at bridge over rte 20, *Stuessy & Gardner 4373* (OS). **Escuintla:** .1 mi N of intersection to El Naranjo on ca-9, *La Duke et al. 528* (OS); 4.8 mi S of intersection of ca-9 & ca-2 on ca-9, *La*

[1]Asterisk indicates chromosome voucher.

Figure 17. Distribution of *Tithonia rotundifolia* in Mexico and Central America.

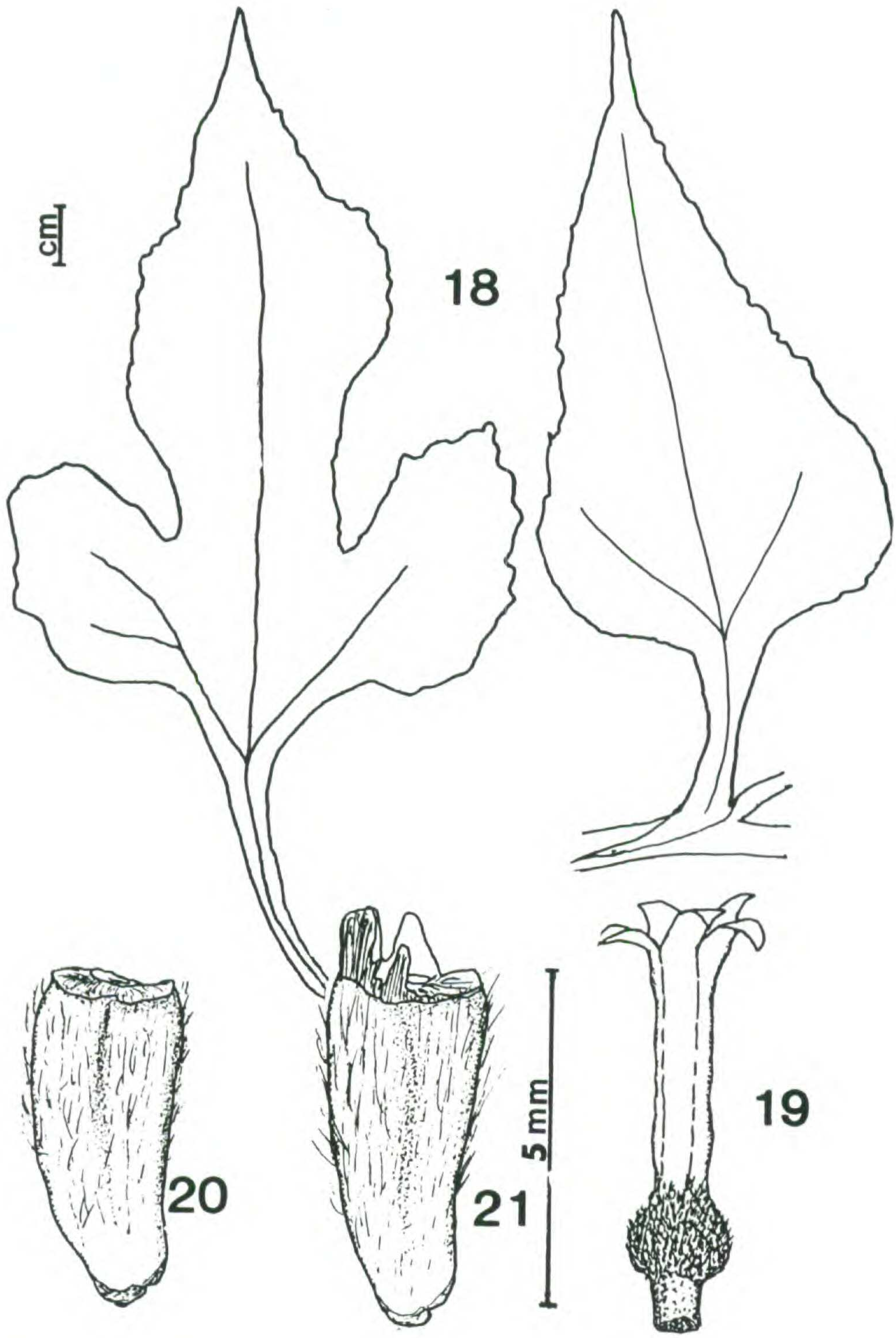
*Duke et al. 529** (OS). **Retalhuleu:** in coffee plantation of Mulua, *Molina 26971* (F, MICH). **San Marcos:** 2.3 mi S jct rd to Malacatán on rte ca-2, *Stuessy & Gardner 4569** (OS). **Zacapa;** Gualán, *Kellerman 5329* (F, OS). HONDURAS. **Comayagua:** ca 15 mi SE of Siguatepeque on rte 1, *Stuessy & Gardner 4417* (OS).

MÉXICO. **Chiapas:** 13 km N of Arriaga along Mex hwy 195, *Breedlove 19855* (OS, MEXU, MICH); Saltillo, *Palmer 558* (GH, K, MO, NY, US). **Colima:** 5 k W of Tecomán just S of intersection of 110 on 200, *La Duke et al. 392** (OS). **Guerrero:** Acapulco & vicinity, *Palmer 631* (OS, F, GH, K, MICH, MO, NY, UC, US); SE edge of Cacahuamilda on Rte 55 toward Taxco, *Stuessy & Gardner 4204** (OS). **Jalisco:** barranca of Tequila, *Pringle 4601* (F, GH, MO, NY, UC, US); W limits of Jalostotitlán on rte 80, *Stuessy & Gardner 4093* (OS); 3–5 mi S of Puerto Vallarta on rd to Tomatlán, *Stuessy & Gardner 4132** (OS); ca 6 mi N of La Resolana (Casimiro Castillo) on rte 80, *Stuessy & Gardner 4135** (OS). **México:** Temascaltepec, *Hinton 1992* (OS, K, MO, NY, US). **Michoacán:** Coalcomán, *Hinton 12452* (GH, K, LL, MICH, NY, UC, US); .7 mi E of rd to Chavinda on hwy 15, S side of rd', *La Duke et al. 393** (OS); 1.9 mi W of Rd to Gómez Farias on hwy 15, *La Duke et al. 480* (OS). **Nayarit:** above La Laguna, a crater lake near Santa Maria del Oro & 30 mi SE of Tepic, *Cronquist 9597* (GH, MICH, MO, NY, TEX, US). **Oaxaca:** 1.7 mi W of Oaxaca-Chiapas line on rte 190, *La Duke et al.* 510A* (OS). **Veracruz:** puente nacional, *Arreguín 2643* (DS, ENCB, F, MICH, NY, TEX). **Yucatán:** Kancabconot, *Gaumer 23524* (C, F, GH, MO, POM, US); Mérida, *Souze 6* (NA).

NICARAGUA. **Granada:** Lake Nicaragua, *Hamblett 1114* (F, GH, MO, NY, SMU, UC). **León:** in open field rt 26 Telica, *Hamblett et al. 210* (F, GH, MICH, MO, NY, SMU, UC). **Madriz:** ca 5 mi E of Honduras-Nicaragua border on rte 1, *Stuessy & Gardner 4436* (OS). **Managua:** rt 1 Tipitapa, *Seymour 2347* (DUKE, GH, MO, NY, SMU, UC). **Zelaya:** in open pasture Bluefields, *Zelaya 447* (F, GH, MO, SMU, UC). NIGERIA. 1 km S Oyo, rd. to Ibadan, Bida, *Bruner 427* (OS). PANAMÁ. Taboga Island, *Celestino 41* (US). RHODESIA. Que Que railway, *Biegel 1043* (K). SAN DOMINGO. without locality, *Wright et al. 267* (US). SAN SALVADOR. Republic of Salvador, *Velasco 8869* (GH, US). UNITED STATES. **Florida:** Tallahassee, *Kral 3739* (FSU, GH). VENEZUELA. **Distrito Federal:** around Caacas, *Pittier 7435* (GH, US). WEST INDIES. HAITI: Haiti, *Ekman 7197* (F, GH, K).

2. **Tithonia brachypappa** Robins. Proc. Amer. Acad. Arts **27:** 174. 1892. TYPE: MÉXICO, San Luís Potosí, Las Palmas, 15 Oct 1890, *C. G. Pringle 3675* (LECTOTYPE, GH!; ISOLECTOTYPES, F (FRAG)!). Figures 18–21.

Erect, annual, herbaceous, 2–3 m tall. Stems round, red to brown to tan, subglabrate to sparsely pilose. Leaves alternate, sessile; blades triangular to 3–5 lobed, 11–21 cm long, 3–11.5 cm wide, at apex acuminate, at base attenuate, auriculate-decurrent on stem, on upper and lower surfaces hispid, at margin serrate. Peduncles 10–30 cm long, 4–7 mm diam, hispid-pilose near head, becoming glabrate below. Heads usually solitary, heterogamous. Receptacle 8–9 mm diam. Phyllaries 15–19, three-seriate, graduated, linear to spathulate; outer bracts 5–9 mm long, 2–3.5 mm wide, at apex



Figures **18–21.** Leaf outlines (**18;** unlobed leaf, *Stuessy and Gardner 4038,* OS, lobed leaf, *Crutchfield and Johnston 5727,* TEX); disk corolla (**19**), outermost disk achene (**20**), and inner disk achene (**21**) of *Tithonia brachypappa.* Figures 19–21, *La Duke and Jansen 418,* OS; same scale.

round with acute tip, minutely pubescent on abaxial surface; inner bracts 12–16 mm long, 4.5–9 mm wide, at apex rounded, minutely pubescent on abaxial surface. Pales striate, 8–12 mm long, 2–2.5 mm wide; apex aristate, 2–5 mm long, usually with lateral lobes. Ray florets 7–8; ligules yellow to orange-yellow, linear, 15–25 mm long, 4–8 mm wide, at apex trifid; tube 1.5 mm long, 0.75–1 mm diam; pappus absent; achenes one-seriate, white to yellow, triangular, sterile. Disk florets 47–70; corollas yellow; corolla lobes 5, 0.75–1 mm long, 0.5–.75 mm wide, at the apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 3–5 mm long, 0.75–1 mm diam, with expanded portion 1 mm long, 1–1.5 mm diam; tube minutely pubescent, 0.75–1 mm long, 0.5–.75 mm diam; anthers black, 4.5 mm long; styles 7–8.5 mm long; stigmas pappillate, 2–3 mm long; pappus lacking on some achenes, fused squamellae on most; achenes fertile, black, brown, or mottled, 4.5–6 mm long, 2–2.5 mm diam, at base (without eliasome). Chromosome number $n = 17$.

PRINCIPAL FLOWERING TIME: September-November (April).
DISTRIBUTION: Tamalipas and San Luis Potosí, Mexico (Fig. 22).

This species can be easily recognized by the decurrent leaf bases. As noted by Blake (1921), the achenes show variation in pappus. The disk achenes on the outside of the head usually have very little, if any, pappus (Fig. 19), but the amount of pappus increased toward the center of the head (Fig. 20). The adaptive significance of this variation is not known.

This taxon is most closely related to *T. rotundifolia* and differs in the following critical characters: 1) pappus of squamellae vs. awns plus squamellae, 2) sessile leaves, with decurrent leaf bases vs. petiolate leaves with attenuate leaf bases, and 3) spathulate phyllaries vs. linear to oblong phyllaries.

REPRESENTATIVE SPECIMENS. MÉXICO. **San Luís Potosí:** limestone hills, Las Palmas, *Pringle 6143* (BM, BR, K, S, UC, US); 10–20 mi W of Ciudad Valles on rte 86, *Stuessy & Gardner 4038* (OS); 2.2 mi E of intersection to El Salto on rte 80, *La Duke et al. 587** (OS). **Tamaulipas:** 6 mi N of Aldama on rd. to Soto La Marina, *Crutchfield & Johnston 5727* (MICH, TEX); .1 mi N of Santa Fé on Hwy 85, *La Duke & Jansen 418** (OS); 40–60 mi S of Ciudad Victoria on rte 101, *Stuessy & Gardner 4033** (OS).

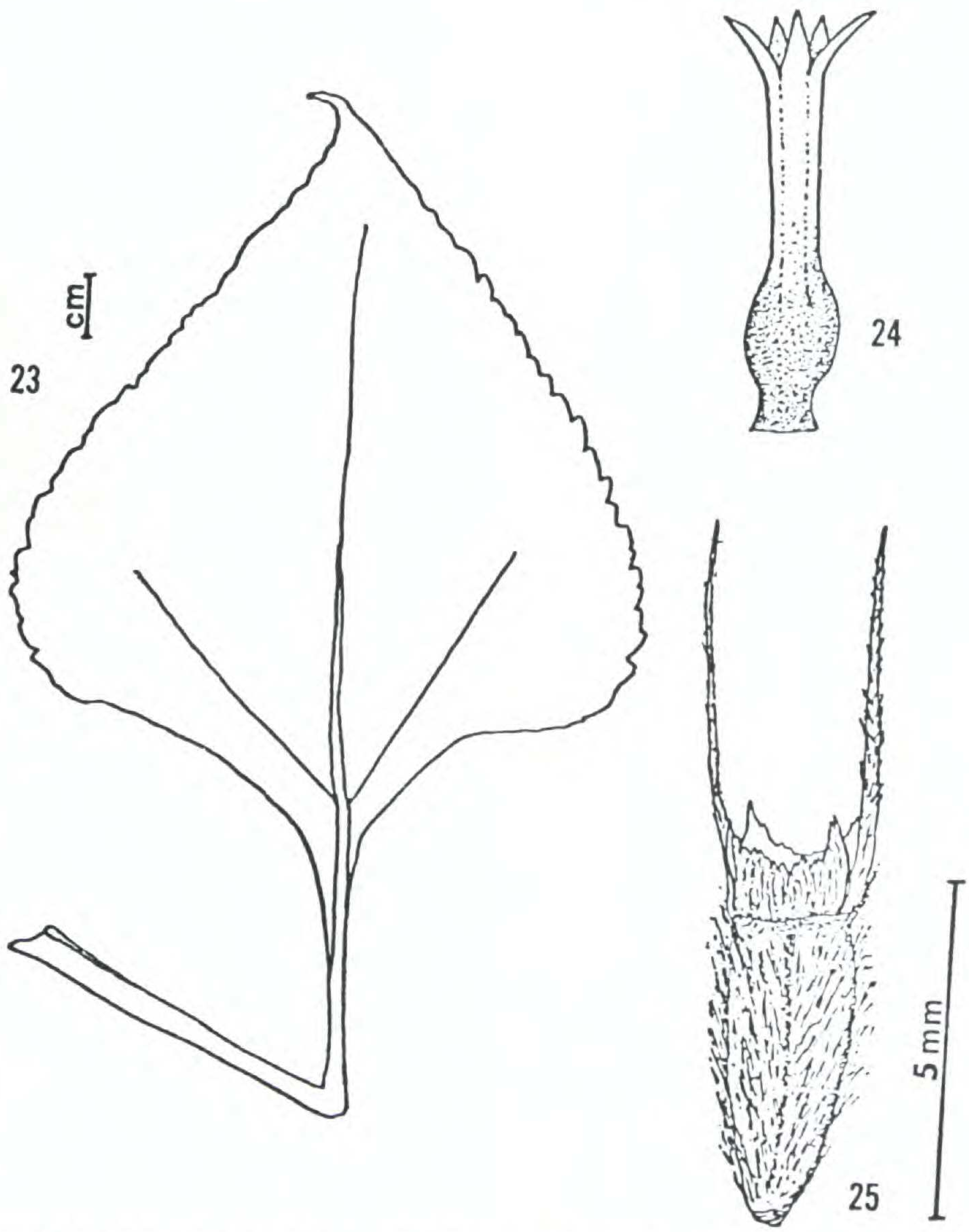
Figure **22.** Distribution in Mexico and adjacent United States of *Tithonia koelzii* (closed triangles), *T. brachypappa* (dots), *T. calva* var. *calva* (circles), *T. calva* var. *lancifolia* (open triangles), *T. calva* var. *auriculata* (closed squares), *T. fruticosa* (asterisks), and *T. thurberi* (open squares).

3. **Tithonia tubaeformis** (Jacq.) Cass. Dict. Sci. Nat. **35:** 278. 1825. Figs. 23–25.

Helianthus tubaeformis Jacq. Pl. Hort. Schonbr. **3:** 65. *pl. 375.* 1798, TYPE: MEXICO, "sub dio floret autumno" (HOLOTYPE, the illustration is taken as the type). Loans were requested from institutions (AWH, BM, CGE, LIV, OXF, and UPS) where Jacquin specimens are known to be (D'Arcy, 1970), but no specimen has been located.

Helianthus tubaeformis Ortega, Nov. Rar. Pl. Horti. Reg. Botan. Matrit. dec. 8. 101. 1798. TYPE: "Nova Hispanae", Flowers in Oct-Nov, *D. de la Cal s.n.* (LECTOTYPE here chosen, M! [photo, OS!]).

Tithonia helianthoides Bernh. Gart. Mag. **2:** 156. *pl. 15.* 1826. TYPE: location, date and collector unknown (HOLOTYPE, the illustration is taken as the type).



Figures **23–25.** Leaf (**23**), disk corolla (**24**), and disk achenes (**25**) of *T. tubaeformis* (*La Duke et al. 406*, OS). Figs. 24 and 25 same scale.

Urbanisol tubiformis (Cass.) Kuntze, Rev. Gen. Pl. **1:** 371. 1891.
Tithonia tubaeformis var. *bourgaena* Pampanini, Bull. Soc. Bot. Ital. **1908:** 134. 1908. TYPE: MEXICO, Valley of Cordoba, 20 Dec 1865-1866, *E. Bourgeau 1566* (HOLOTYPE, FI! [photo OS!]).

Erect, annual, herbaceous, 1–3 m tall. Stems round, red to yellow to tan to brown, moderately to densely pubescent. Leaves alternate with petioles 2–11 cm long; blades deltate, 5–25 cm long, 6–17 cm wide, at apex acuminate, at base attenuate, on upper surface strigose-hirsute, on lower surface hirsute to villous, at margin crenate to serrate. Peduncles 10–45 cm long, 4–12 mm diam, moderately to densely pubescent. Heads usually solitary, heterogamous. Receptacle 8–25 mm diam. Phyllaries 15–25, two-seriate, graduated, linear to oblong (oblanceolate); outer bracts 15–30 mm long, 2–5 mm wide, at apex acute, on abaxial surface moderately pubescent; inner bracts 14–24 mm long, 3–4 mm wide, at apex acute, abaxial surface minutely pubescent. Pales striate, tan to purple, 10–18 mm long, 2–3.5 mm wide; apex acuminate to aristate, 3–9 mm long, usually with lateral lobes, minutely pubescent above. Ray florets 11–18; ligules yellow, oblong to ovate, 14–45 mm long, 5–15 mm wide, at apex trifid; tube 1.5–3 mm long, 0.75–1 mm diam; pappus absent or short scales; achenes one-seriate, triangular, white-tan, sterile. Disk florets (30–) 90–120; corollas yellow; corolla lobes 5, 1 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 3–5 mm long, 1–2 mm diam, with expanded portion 1–2 mm long, 1–2 mm diam; tube minutely pubescent, 0.25–1 mm long, 0.5–.75 mm diam; anthers black, (4–) 5 mm long; styles 4.5–9 mm long; stigmas pappillate, 1–3 mm long; pappus of fused squamellae with or without two awns; achenes fertile, brown, black, or mottled, pubescent, quadrangular, 4–6 mm long, 1.75–3 mm diam, smooth at base without an eliasome. Chromosome number $n = 17$.

PRINCIPAL FLOWERING TIME: August-November.

DISTRIBUTION: Weedy habitats throughout most of tropical Mexico, south to Panama (Fig. 26).

Tithonia tubaeformis is a weedy annual occurring throughout most of Mexico and Central America, often in cultivated or fallow fields. It is quite variable morphologically, but easily recognized by the linear, pubescent phyllaries, deltate leaves, and large annual habit. *Tithonia tubaeformis* hybridizes with *T. rotundifolia* in the field to produce F_1 hybrids with intermediate morphology and low fertility (see cytology section).

Tithonia tubaeformis is most closely related to *T. thurberi*, but is not known to be sympatric with it. *Tithonia tubaeformis* differs in possessing the following characters: 1) greater number of disk florets, 2) larger habit, 3) linear phyllaries vs. oblong to ovate phyllaries, and 4) a more widespread distribution (Fig. 22 vs. 26).

Figure **26.** Distribution of *Tithonia tubaeformis* in Mexico and Central America.

REPRESENTATIVE SPECIMENS. GUATEMALA. **Chiquimula:** dry thickets and pine forest btwn Jocotán and Camotán, *Molina 25216* (C, F, NY, US). **Huehuetenango:** on the ruins of Zaculen, *Skutch 1593* (F, GH, LL); 4–5 mi S Huehuetenango, rte ca-1, *Stuessy & Gardner 4325** (OS). **Jutiapa:** btwn Jutiapa and La Calera SE of Jutiapa, *Standley 76071* (F). **Sacatepequez:** 4 mi E El Tajar on rte ca-1, *La Duke et al. 533* (OS). **Santa Rosa:** Chupadero, *Heyde 4202* (F, GH, K, NY, US). MÉXICO. **Chiapas:** S of center of Amatenango del Valle, Municipio of Amatenango del Valle, *Ton 1066* (DS, DUKE, ENCB, F, MICH, NY). **Chihuahua:** NW of Chihuahua, *Lesueue 348* (ARIZ, F, GH, MO, TEX); Parral and vicinity 10 mi SE, *Gentry 17916* (LL, US). **Colima:** without locality, *Palmer 1220* (MICH, MO, NY, UC, US). **Distrito Federal:** Ciudad de México, *Arvizu 87* (ENCB). **Durango:** city of Durango and vicinity, *Palmer 690* (C, F, GH, K, MO, NY, UC, US); 9.2 mi SW Francisco I Madero on hwy 40, *La Duke et al. 380** (OS); .9 mi W of Leo Guzmán on hwy 40, *La Duke et al. 372A* (OS). **Hidalgo:** 2.6 mi S Trancas on rte 86, *La Duke et al. 580A* (OS). **Jalisco:** W limits of Jalostotitlán on rte 80, *Stuessy & Gardner 4094** (OS); ca. 5 mi NW Tequila on rte 15, *Stuessy & Gardner 4101** (OS); ca 26 mi NW Tequila on rte 15, *Stuessy & Gardner 4108** (OS); 1 mi N rd to Teocitatlán on hwy 33, *La Duke et al. 472** (OS). **México:** .3 mi W Tlapizahuac, *La Duke & Jansen 398** (OS); .5 mi S of Tenancingo on rte 55, *Stuessy & Gardner 4195** (OS). **Michoa-**

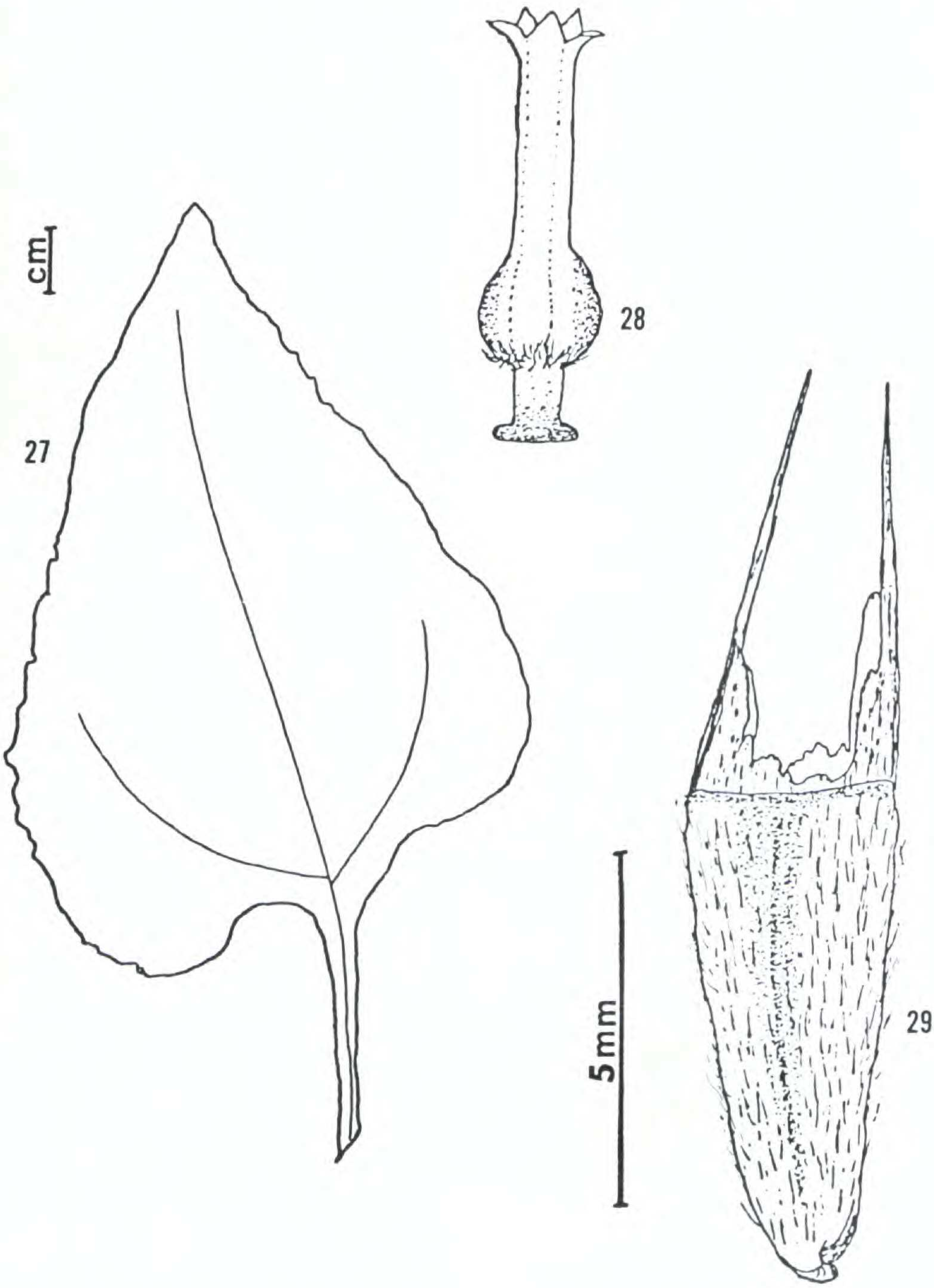
cán: Sierra Torricillas Coalcomán, *Hinton 12358* (GH, LL, MICH, NY, UC, US); 1.9 mi W of rd to Gómez Farías on hwy 15, *La Duke et al. 481** (OS). **Morelos:** valley Jojutla, *Pringle 9306* (F, GH, LL, MICH, NY, SMU, TEX, US, YU). **Nayarit:** Tepic, *Palmer 1851* (F, GH, NY, US); .6 mi S of hwy 15 & rd to Uzeta, *La Duke et al. 390** (OS). **Oaxaca:** .1 mi E of rd to Chivala on hwy 185, *La Duke & Jansen 406** (OS); 3.9 mi E of rd to La Mata on hwy 185, *La Duke & Jansen 407** (OS); between Huajuapán de León & Yanhuitlan, *Stuessy & Gardner 4249** (OS); 1 mi W Las Minas on rte 190, *La Duke et al. 509** (OS); 1.7 mi W Oaxaca-Chiapas border on rte 190, *La Duke et al. 511** (OS). **Puebla:** along rt 115 just SE of Morelos-Puebla border, *King 2920* (DS, MICH, NY, TEX, UC, US); 2.0 mi NE of rte 150 on rte 125, *La Duke et al. 570** (OS). **San Luís Potosí:** near Arriaga on rte 80, *Stuessy & Gardner 4075* (OS). **Sinaloa:** .3 mi W El Zapotillo on rte 40, *La Duke et al. 429* (OS). **Tamaulipas:** near San Vicente, *Von Rozynski 201* (F, MICH, NY). **Veracruz:** El Marzo, NW of Santa Ana Atzacán, *Rosas 271* (DS, GH, LL, MICH, MO).

4. **Tithonia thurberi** A. Gray, Proc. Amer. Acad. Arts **8:** 655. 1873. TYPE: MÉXICO, Sonora, Magdalena, Oct 1851, *G. Thurber 910* (HOLOTYPE, GH!; ISOTYPES, GH!, K, [photo, OS!], MO!, NY!). Figs. 27–29.

Tithonia palmeri Rose, Contr. U.S. Nat. Herb. **1:** 104. 1891. TYPE: MEXICO, Sonora, along watercourses and in canyons, Alamos, Sept 1890, *E. Palmer 721* (LECTOTYPE here chosen, US!; ISOLECTOTYPES, DS!, F!, GH!, K [photo, OS!], NY!, UC!, US!).

Urbanisol thurberi (A. Gray) Kuntze, Rev. Gen. Pl. **1:** 371. 1891.

Erect, annual, herbaceous, 0.7–2 m tall. Stems round, tan, glabrous to hirsute. Leaves alternate, with petioles 33 mm long or sessile; blades deltate, 7–28 cm long, 5.5–21.5 cm wide, at apex acuminate, at base attenuate, on upper surface sparsely hirsute, on lower surface hirsute with larger hairs on veins, at margin serrate. Peduncles 17–36 cm long, 3.5–6 mm diam, sparsely to moderately pubescent near the head. Heads solitary, heterogamous. Receptacle 7–11 mm diam. Phyllaries 13–16, three-seriate, slightly graduated, linear to spathulate; outer bracts 8–15 mm long, 2.5–4.5 mm wide, at apex acute, on abaxial surface minutely pubescent; inner bracts 12–15.5 mm long, 3.5–7 mm wide, at the apex acute, on abaxial surface glabrous. Pales striate, 11–16.5 mm long, 2–4 mm wide; apex acuminate, 3 mm long, usually with lateral lobes, glabrous. Ray florets 7–10; ligules yellow, oblong, 9–15 mm long, 4–6 mm wide, at apex trifid; tube 0.75–1.5 mm long, 0.5–.75 mm diam; pappus absent; achenes one-seriate, triangular, white-tan, sterile. Disk florets 40–60; corollas yellow; corolla lobes 5, 0.75–1 mm long, 0.5–.75 mm wide, at the apex acute; throat cylindrical with expanded minutely



Figures **27–29.** Leaf (**27**), disk corolla (**28**), and disk achene (**29**) of *Tithonia thurberi (Gentry 1830,* LL). Figures 28 and 29 same scale.

pubescent base, with cylindrical portion 3–4 mm long, 1–1.5 mm diam, with expanded portion 1–1.5 mm long, 1.2–2 mm diam; tube minutely pubescent, 1–1.75 mm long, 0.5–.6 mm diam, thickened; anthers black (brown), 2–4 mm long; styles 4–7.5 mm long; stigmas pappillate, truncate, 0.75–1.5 mm long; pappus laterally fused squamellae and two awns; achenes fertile, triangular (or quadrangular), 6–9 mm long, 1.75–3 mm diam, smooth at base without eliasome. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: August-September (dependent on local rainfall).

DISTRIBUTION: Confined to xeric northern Sonora, Mexico and southern Arizona, U.S.A. (Fig. 17).

Tithonia thurberi, an annual, is one of the smaller taxa. It is limited in distribution and distinctive in its long pubescence on the veins of the leaves and broad pales enclosing long (6–9 mm) achenes.

REPRESENTATIVE SPECIMENS. MÉXICO. **Chihuahua:** Guasaremos, Río Mayo, *Gentry 1830* (ARIZ, F, GH, K, LL, MEXU, MO, NA, NY, UC, US). **Sonora:** on rd from Libertad to Datil, 8.6 mi from Serna-Libertad fork, *Wiggins 6100A* (DS); 31 mi S of Nogales, *Shreve 6607* (F); 31 mi S of Nogales, along Río de Los Alisos, *Wiggins 7023* (ARIZ, DS); open park-like flat 10 mi S of Santa Ana, *Wiggins & Reed 7203* (DS, MO, TEX, US); canyon of Agua Amarga, *White 3645* (ARIZ, GH, MICH); Horconcitos, Río Huachinera, *White 3717* (GH, MICH); 19 mi N of Colorado on rd to Mazatlán, *Wiggins 357* (DS, GH, MICH, MO, NA, NY, US); Benjamin Hill, *Gentry 17859* (LL, US); ca 4 mi E of Álamos along rd to Milpillas, *Henrickson 2429B* (RSA); La Pasión, 15 km NE of Tubutama, *Arizpa 99* (ENCB); 2 mi N of Los Janos on hwy 15, *La Duke et al. 421** (OS). UNITED STATES. **Arizona:** Helvetia, *Thornber 7226* (ARIZ, SMU); Baboquivari Canyon, *Peebles et al. 411* (ARIZ); Tumacacori Mission, *Peebles & Harrison 4666* (ARIZ, NA); Baboquivari Mtns, *Jones 25121* (DS, GH, LL, NA, POM, TEX, UC); Toro Canyon, Baboquivari Mtns, *Gilman 51* (ARIZ, DS, GH, NA); Toro Canyon, *Kearney & Peebles 10455* (ARIZ, LL, POM); 5 mi SW of Patagonia, *Benson 10414* (ARIZ); 7 mi W of US 89 toward Ruby, *Barr 68-S74* (ARIZ); just W of I 19 on AZ rte 289, *Keil & Pinkava K11095* (LL, OS); ca 5 mi NE of Nogales along a local rd just off hwy 82, *Urbatsch 2848* (OS).

2. Series *Grandiflorae* La Duke. Rhodora **84:**140. 1982.

Plant perennial shrubs or trees; leaves petiolate, blades deltate or lobate; ligules more than 45 mm long. Species 5 and 6. TYPE: *Tithonia koelzii* McVaugh.

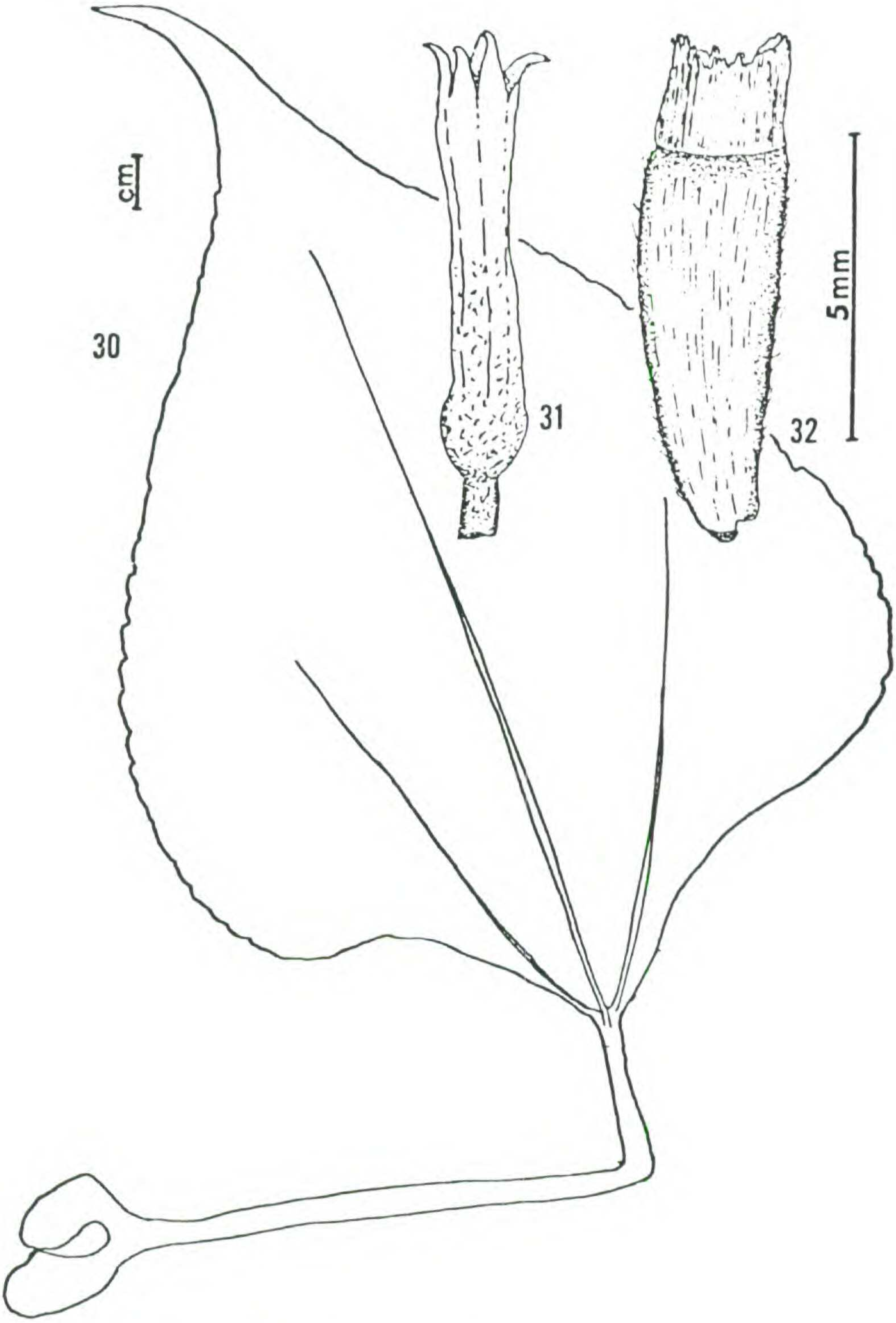
5. **Tithonia koelzii** McVaugh, Contr. Univ. Michigan Herb. **9:** 443. 1972. TYPE: MÉXICO. Jalisco, 12–13 km SE Pihuamo, 500–600m, 15 Dec 1959, *R. McVaugh & W. N. Koelz 1795* (HOLOTYPE, MICH!; ISOTYPES, DUKE!, ENCB!, LL!, NY! US!). Figures 30–32.

Erect, perennial tree, 6–7 m tall. Stems round, brown, 15 cm DBH, sparsely pubescent to glabrous. Leaves alternate with petioles 50–120 mm long with ephemeral auriculae at base; blades deltate, 9.5–19 cm long, 5.8–7 cm wide, at apex acuminate, at base cuneate, on upper and lower surface moderately hispid, at margin crenate. Peduncles 9–12 cm long, 2–4 mm diam, sparsely pubescent to glabrous near head. Heads usually solitary, heterogamous. Receptacle 8–9 mm diam. Phyllaries about 20, three-seriate, graduated, linear to lanceolate; outer bracts 7 mm long, 4 mm wide, at apex acuminate, on abaxial surface glabrous to minutely pubescent; inner bracts 20 mm long, 6 mm wide, at apex rounded, on abaxial surface glabrous to minutely pubescent. Pales striate, 11 mm long, 2 mm wide; apex aristate, 3 mm long, usually with lateral lobes, minutely pubescent. Ray florets 11; ligules yellow, linear, 45 mm long, 17 mm wide, at apex trifid; tube 1.5 mm long, 0.75 mm diam; pappus absent or some scales; achenes one-seriate, dark brown, sterile. Disk florets about 60; corollas yellow; corolla lobes 5, 1.5 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 4.5–5 mm long, 1–1.5 mm diam, with expanded portion 1.5 mm long, 1.5 mm diam; tube minutely pubescent, 1 mm long, 0.5 mm diam; anthers tan, 5 mm long; styles 11.5 mm long; stigmas pappillate, 3.5 mm long; pappus ring of fused squamellae; achenes fertile, black, brown, pubescent, particularly on the edges, quadrangular, 6.5–7 mm long, 3 mm diam, at base smooth without eliasome. Chromosome number $n = 17$ (counted as $2n = 34 + 4\text{–}5$ B).

PRINCIPAL FLOWERING TIME: October to November.

DISTRIBUTION: Known only from the type locality in Jalisco, México (Fig. 33).

Tithonia koelzii is a small tree, and the peduncle is the least flared of all taxa of the genus. *Tithonia koelzii* is one of two taxa, the other *T. diversifolia*, with auriculae at the base of the petiole which are ephemeral. These laminar auriculae are produced on older mature



Figures **30–32.** Leaf (**30;** *La Duke et al.* 477, OS), disk corolla (**32**), and disk achene (**31**) of *Tithonia koelzii.* Figs. 31 and 32; *McVaugh and Koelz 1504* (MICH); same scale.

Figure 33. Distribution of *Tithonia pedunculata* (triangles), *T. diversifolia* (dots), and *T. longiradiata* (circles) in Mexico and Central America.

leaves, and when the plants are stressed, they dry and brown, and may be difficult to detect. Chromosomally, *T. koelzii* is diploid at $n = 17$, but has an additional complement of 5 to 6 B-chromosomes.

REPRESENTATIVE SPECIMENS. MÉXICO. **Jalisco:** 12–13 km SW of Pihuamo, 500–600m, *McVaugh & Koelz 1504* (DUKE, ENCB, MICH, NY), *McVaugh 24496* (DUKE, ENCB, LL, MICH), *La Duke et al. 477** (OS).

6. **Tithonia diversifolia** (Hemsl.) A. Gray, Proc. Amer. Acad. Arts **19:** 5. 1883 Figures 34–36.

Mirasolia diversifolia Hemsl. in Godman & Salvin, Biol. Centr. Amer. Bot. **2:** 168. *t. 47.* 1881. TYPE: MÉXICO, Veracruz, Valley of Orizaba, 12 May 1866, *E. Bourgeau 2319* (LECTOTYPE, K!, [photo, OS!]; ISOLECTOTYPES, BR!, FI!, GH!, S!, US!).

Urbanisol tagetifolius var. *diversifolius* f. *grandiflorus* O. Kuntze, Rev. Gen. Pl. **1:** 370. 1891. TYPE: Singapore, date unknown, probably collected by *O. Kuntze s.n.* (HOLOTYPE, not located). This taxon is placed here based on specimens annotated by Kuntze.

Urbanisol tagetifolius var. *flavus* O. Kuntze, Rev. Gen. Pl. **1:** 1875. TYPE: Singapore, Oct 1875, *O. Kuntze 6074* (HOLOTYPE, NY!; ISOTYPE, K!).

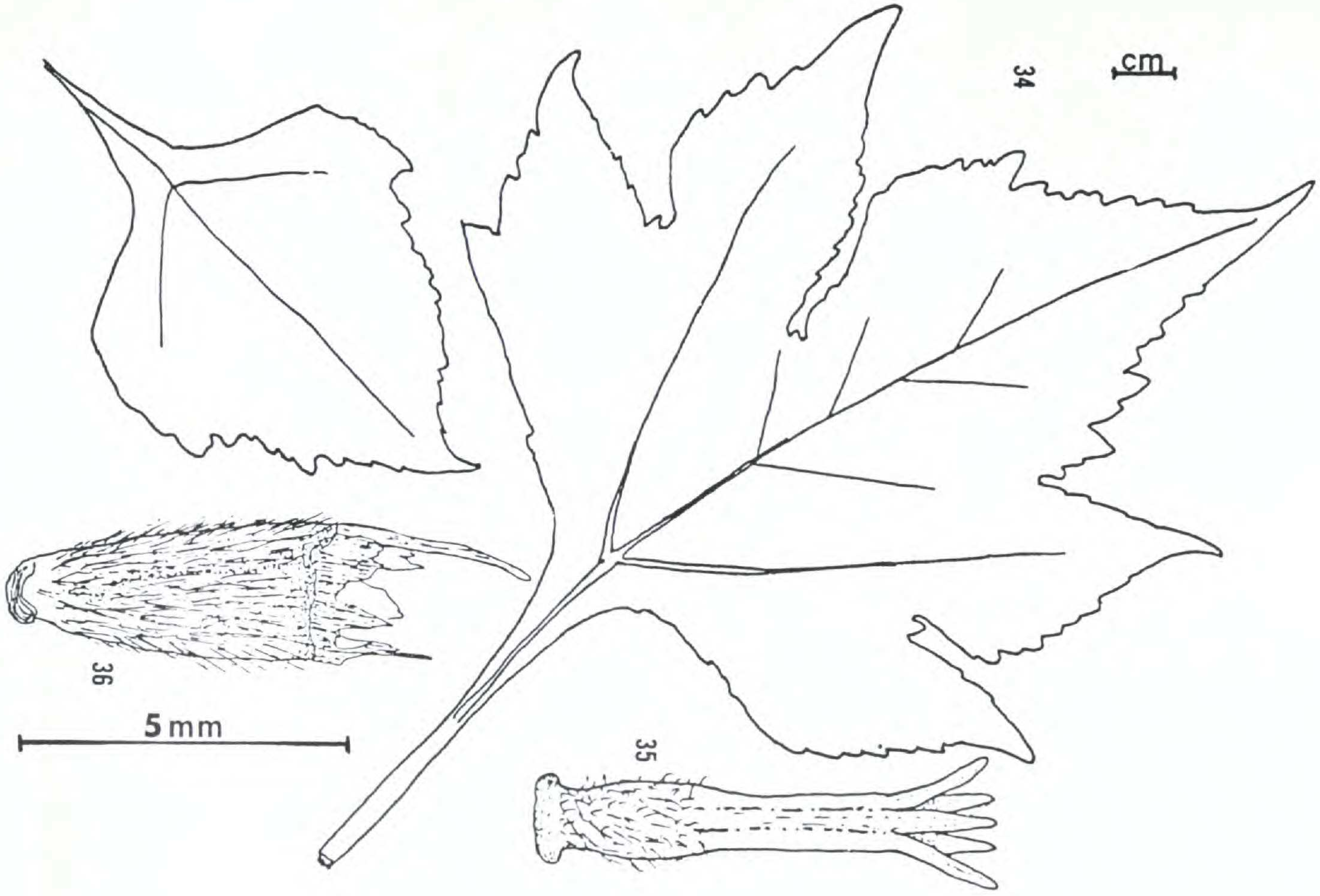
Urbanisol tagetifolius var. *diversifolius* (Hemsl.) O. Kuntze, Rev. Gen. Pl. **1:** 371. 1875.

Tithonia trilobata Sch.-Bip. in Klatt, Bull. Soc. Bot. Belg. **31:** 203. 1891. *Nom. nud. pro. syn.* Based on the following cited specimen: Mirador, Nov 1841, *F. M. Liebmann 603* (C!, P!, [photo, OS!]).

Helianthus quinquelobus Sesse & Mocino, Fl. Mex. ed. 2. 193. 1894. TYPE: MÉXICO, Veracruz, Orizaba, *M. Sesse & J. M. Mocino s.n.* [Madrid herb. 2936] (LECTOTYPE here chosen; M!).

Tithonia diversifolia var. *glabriscula* S. F. Blake, Contr. U.S. Nat. Herb. **20:** 435. 1921. TYPE: MÉXICO, Oaxaca, N of Tuxtepec, 90 m, 9 Apr 1894, *E. W. Nelson 346* (HOLOTYPE, US!).

Erect, perennial, herbaceous, 2.5–5 m tall. Stems round, usually brown to green, glabrous to villous. Leaves alternate, sessile or with petioles to 6 cm long; blades deltate to 3–5 lobed, 7–33 cm long, 7–22 cm wide, at apex acuminate, at base attenuate, ephemeral auricle at base of petiole, on upper surface glabrous to hispid-pilose, on lower surface glabrous to villous, at margin serrate. Peduncles 7–24 cm long, 4–13 mm diam, sparsely tuberculate-hispid. Heads usually solitary, heterogamous. Receptacle 7–13 mm diam. Phyllaries 16–28, (three-) four-seriate, graduated, oblong to ovate, outer bracts 6–10 mm long, 4–7 mm wide, at apex rounded to acute, occasionally scarious, on abaxial surface usually glabrous; inner bracts 10–20 mm long, 3–10 mm wide, at apex rounded to acute, on abax-



Figures **34–36.** Leaf outlines (**34**, *La Duke et al. 569a*, OS), disk corolla (**35**), and disk achene (**36**) of *Tithonia diversifolia*. Figures 35 and 36, *Feddema 2889*, TEX; same scale.

ial surface glabrous. Pales striate, 10–13 mm long, 2–3 mm wide; apex aristate, 1.5–2.5 mm long, usually with lateral lobes, minutely pubescent occasionally toward apex or on fold. Ray florets 7–14; ligules yellow, linear, 48–69 mm long, 9–16 mm wide, at apex trifid; tube 2–2.5 mm long, 1–1.5 mm diam; pappus absent or paleaceous ring; achenes one-seriate, white to yellow, sterile. Disk florets 80–120; corollas yellow; corolla lobes 5, 1–1.5 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 3–4 mm long, and 0.75 mm diam, with expanded portion 1.5–3 mm long, 1–1.5 mm wide; tube partially minutely pubescent, 0.75–1 mm long, 0.75 mm diam; anthers black, 4–5 mm long; styles 9–12 mm long; stigmas pappillate, 2–3 mm long; pappus of fused squamellae, 2 subequal awns; achenes fertile, black or mottled, puberulent, quadrangular, 5–6 mm long, 1.5–2 mm diam at base smooth without eliasome. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: September to January.

DISTRIBUTION: Tropical México and Central America (Fig. 33).

Tithonia diversifolia is the most widespread of the taxa of *Tithonia*. It has been successfully cultivated in Africa, Australia, Asia, and North America where it has escaped and is now locally abundant. It is a weedy herbaceous perennial, most closely related to *T. koelzii* (see *T. koelzii* for discussion), but it most often is confused with *T. rotundifolia* because of its similar 3–5 lobed leaves and hearty habit.

REPRESENTATIVE SPECIMENS. AUSTRALIA. **N. Queensland:** near Tolga, *McKee 9394* (K). **New South Wales:** Coffs Harbor, *Covney 9426* (RSA). BERMUDA. Harrington House Garden, *Brown et al. 2267* (NY). BRITISH NORTH BORNEO. Sandakan, *Wood 1164* (UC). BURMA. Rangoon, *Dickason 5234* (GH). CAMEROON. 10 km S of Ngaoundere, *Amshoff 256* (K). CANARY IS. **Tenerife:** Puerto de Guimar, *Hansen 1036* (C). COSTA RICA. **Heredía:** along rd to Concepción, ca 2 km N of San Isidro, *King 6793* (F). **San José:** Tabarcía, *Jimenez 655* (CR, F, NY). CUBA. Pinar del Río, *Alain & Killip 2026* (NY, US). DOMINICAN REPUBLIC. Santiago, *Jiménez 975* (US). EL SALVADOR. **Ahuachapán:** Ataco, *Standley & Padilla 2646* (F). GHANA. no locality, *Akpabla 1962* (K). GUATEMALA. Antigua, *Holiway 65* (GH). **Alta Verapaz:** .5 mi NE of San Pedro Carchá on rd to Sebol, *Jansen & Harriman 526* (OS). **Chiquimula:** 2.6 mi SE Quezaltepeque, *La Duke et al. 531* (OS). **Huehuetenango:** 24 mi NW Huehuetenango on rte ca-1, *La Duke et al. 535** (OS). **Quezaltenango:** below Santa María de Jesús, *Jansen & Harriman 521* (OS). HONDURAS. **Choluteca:** between El Chinchayote and Comali, *Molina 24581* (MO, NY, US). **Morazán:** ca 18 mi S of Tegucigalpa on rte 1, *Stuessy & Gardner*

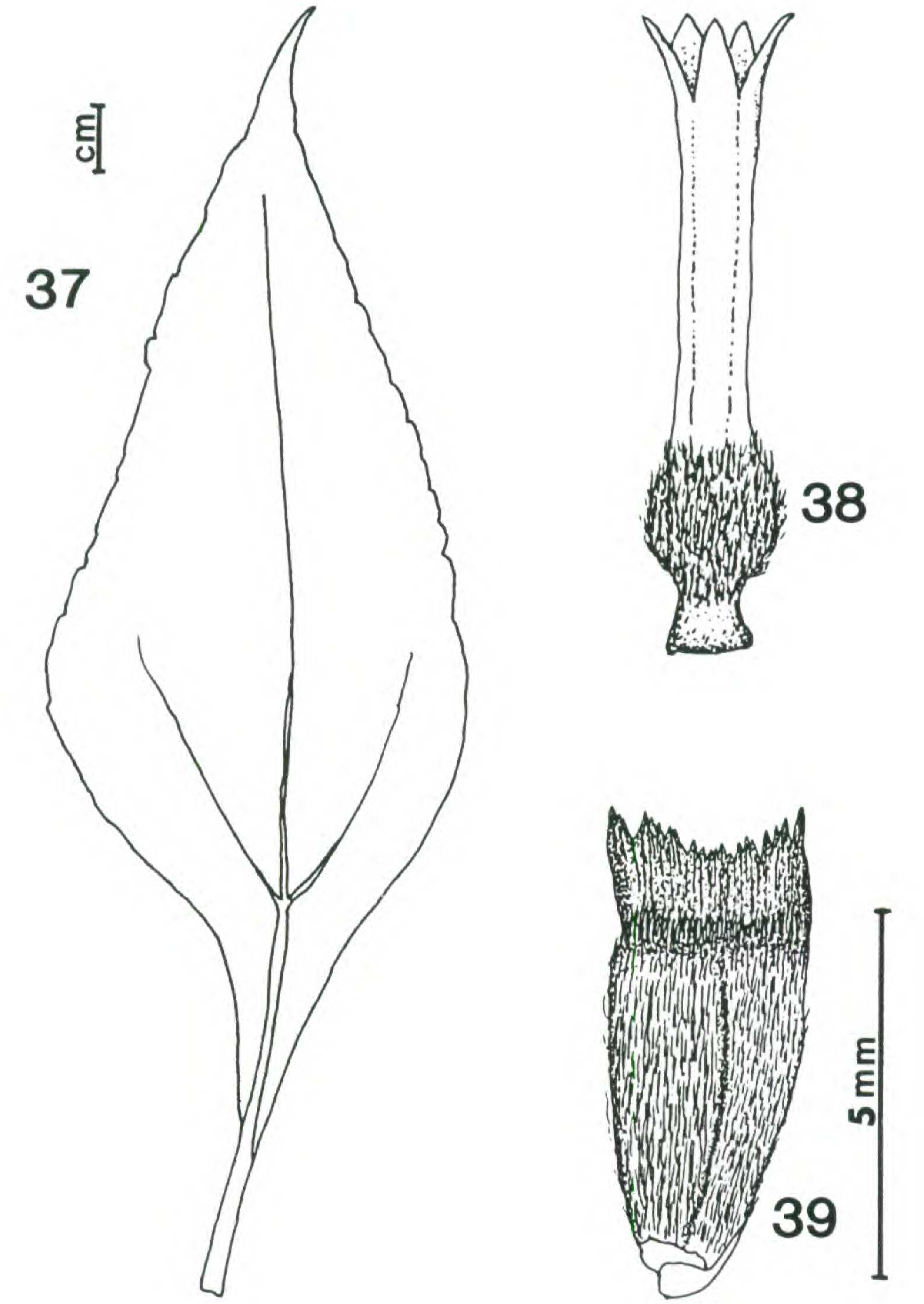
4424 (OS). INDIA. **Assam:** Bamanigaon, *Chand 2496* (UC). INDOCHINA. Gourane, *Poilane 1442* (UC). IVORY COAST. Gagnoa, *Sundell 289* (NA). KENYA. Mutuati-Nyambeni Highlands, *Hanid & Kiniaruh 1003* (MO). MALAWI. **Dedza:** Dedza, *Brummit 10415* (K). MALAYSIA. **Malacca:** no locality, *Vesterdal 397* (C). MÉXICO. **Chiapas:** about 23 mi W of San Cristóbal de las Casas, *Cronquist 9674* (GH, MICH, MO, NY, TEX, US); ca 20 mi E of Tuxtla Guitérrez on rte 190, *Stuessy & Gardner 4299* (OS); 6.5 mi W of Apaz on rte 190, *La Duke et al. 523** (OS). **Guerrero:** Cruz de Ocote, ca 25km SWS of Camolta, *Feddema 2889*, (DS, DUKE, ENCB, MO, MICH, NY, TEX); **Oaxaca:** Chiltepec, *Calderon 446* (GH, LL, MEXU, UC, US); .2 mi N of Tuxtepec, *La Duke & Jansen 403** (OS). **Tabasco:** 4.7 mi E of Cárdenas on rte 180, *La Duke et al. 564** (OS). **Veracruz:** Btwn San Andres Tuxtla and Catemaco, *Cronquist & Sousa 10360* (DS, DUKE, ENCB, GH, MEXU, MICH, NY, TEX, US); 1.1 mi E of rd to Cuautlapan on rte 150, *La Duke et al. 568a* (OS). **Yucatán:** Mérida, *Sousa 5* (NA). NIGERIA. **Calabar:** Calabar, *Daramola 55325* (K). PANAMA. **Cocle:** 1.9 mi S of El Valle, *Stuessy & Gardner 4529* (OS). PHILIPPINES. **Mindoro Is:** Puerto Galera, *Velasquez 25* (GH). PUERTO RICO. along rd near Florida, *Wagner 791* (A). S. RHODESIA. **Umtali:** no locality, *Chase 4632* (K, MO). SEYCHELLE IS. Victoria, *Jeffrey 750* (K). SRI LANKA. Peradeniya, *Comandor 318* (MO). SUMATRA. Vicinity of Rantau, *Toroes 1941* (DS, VC). TAHITI. rd. between Papeete & Papeari, *Setchell & Parks 227* (GH, UC). TANZANIA. roadside near Chemka, *Baagoo et al. 159*. (C). THAILAND. Bangkok, *Sorensen et al. 1986* (C, K). TRINIDAD. Blanchisseuse Rd, *Ross 1020* (A). UNITED STATES. **Florida:** Hernando City, Chinsegut Hill, *Colley 6333* (FSU); ca 3 mi W Brooksville, Fla 50, *Beckner 796* (FSU, GH). **Hawaii:** Lawai Valley, *Herbst 2270* (GH); E Manoa rd, Honolulu, *Bush 107* (NA). WEST INDIES. HAITI: Bodarie to Thiote, *Holdridge 2036* (MICH, NY, US). ZAIRE. environs of Lubumbashi, *Quarre 5400* (MO).

3. Series *Fruticosae* La Duke. Rhodora **84:**140–141. 1982.

Plants perennial shrubs; leaves lanceolate, sessile or petiolate; phyllaries in 3 or 4 series; achenes quadrangular. Species 7 and 8. TYPE: *Tithonia fruticosa* W. M. Canby & J. N. Rose in J. N. Rose.

7. **Tithonia fruticosa** W. M. Canby & J. N. Rose in J. N. Rose, Contr. U.S. Nat. Herb. **1:** 104. *pl. 5*. 1891. TYPE: MÉXICO, Sonora, among bushes near a watercourse, Alamos, Mar – Apr 1890, *E. Palmer 303 (*LECTOTYPE here chosen, US!; ISOLECTOTYPES, A!, GH!, K [photo, OS!], NY!, US!).
Figures 37–39.

Erect, perennial, shrub, 2–3 m tall. Stems round, gray to brown, minutely soft-woolly. Leaves alternate, sessile or with petioles to 30 mm long; blades lanceolate-deltate, 9–23 cm long, 4.5–9 cm wide, at apex long acuminate, at base attenuate, on upper and lower surfaces soft-woolly, at margin serrate to crenate. Peduncles



Figures **37–39.** Leaf (**37**), disk corolla (**38**), and disk achene (**39**) of *Tithonia fruticosa (Weber & Bye 8352,* os). Figures 38–39, same scale.

5.4–12 cm long, 4–7 mm diam, densely woolly. Heads usually solitary, heterogamous. Receptacle 10–15 mm diam. Phyllaries about 24, four-seriate, graduated, ovate; outer bracts 9–14 mm long; 5–11.5 mm wide, at apex rounded, on abaxial surface minutely soft-pubescent; inner bracts 14–21 mm long, 5–8.5 mm wide, at apex rounded, on abaxial surface minute soft-pubescent. Pales striate, 11.5–15 mm long, 1.5–3 mm wide; apex acute to aristate, 3–5 mm long, usually with secondary lobes, usually minutely hispid apically. Ray florets 14–19; ligules yellow, linear, 25–41 mm long, 5.5–11 mm wide, at apex trifid; tube 3 mm long, 0.75–1.5 mm diam; pappus absent; achenes one-seriate, yellow to brown, sterile. Disk florets 100–120; corollas yellow above, dark below; corolla lobes 5, 1–1.25 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 4–5 mm long, and 0.75–1 mm diam, with expanded portion 1.5–2 mm long, and 1–1.75 mm diam; tube minutely pubescent, 1–2 mm long, 0.75–1 mm diam; anthers tan, 4.5–5 mm long; styles 9–12 mm long; stigmas pappillate, 2–4 mm long; pappus of fused squamellae; achenes fertile, gray to brown to black, pubescent, quadrangular or subquadrangular, 4.5–6 mm long, 2–2.5 mm diam, smooth at base without eliasome. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: March-April.

DISTRIBUTION: Canyons and slopes in the Mexican states of Chihuahua, Durango, Sinaloa, and Sonora, usually near water (Fig. 22).

Tithonia fruticosa is a weak perennial shrub which branches from the base. It is easily recognized by its lanceolate, acuminate-tipped leaves which, like the branches, are densely soft-pubescent, and by its broadly ovate phyllaries. *Tithonia fruticosa* is restricted in distribution to northwestern Mexico, where it grows in mesic habitats.

REPRESENTATIVE SPECIMENS. MÉXICO. **Chihuahua:** near Batopilas, *Goldman 232* (US); Sierra Orejon Río Mayo upper Sonora, *Gentry 1219* (F, NA); Barranca del Cobre, *Knobloch 7031* (US); Barranca del Cobre, S wall of Guacaybo arroyo, *Hewitt 21* (GH); downslope from Guageybo, *Pennington 57* (TEX); La Bufa, SE of Creel, *Knobloch 512* (SMU); Santa Rose, *Pennington 337* (TEX); La Bufa, *Weber & Bye 8352** (OS). **Durango:** San Ramon, *Palmer 68* (F, MO, NA, NY, UC, US); Tayoltita, *White 5002* (MICH). **Sinaloa:** Sierra de Los Álamos, *Palmer 303* (A, GH, NY, US); Puerta a Tamiapa, *Gentry 5845* (ARIZ, GH, MICH, MO, NA, NY). **Sonora:** Huchuerachi, *Hartman 301* (GH, NY); vicinity of Álamos, *Rose 13085* (C, F, GH, MO, NY, US); canyon

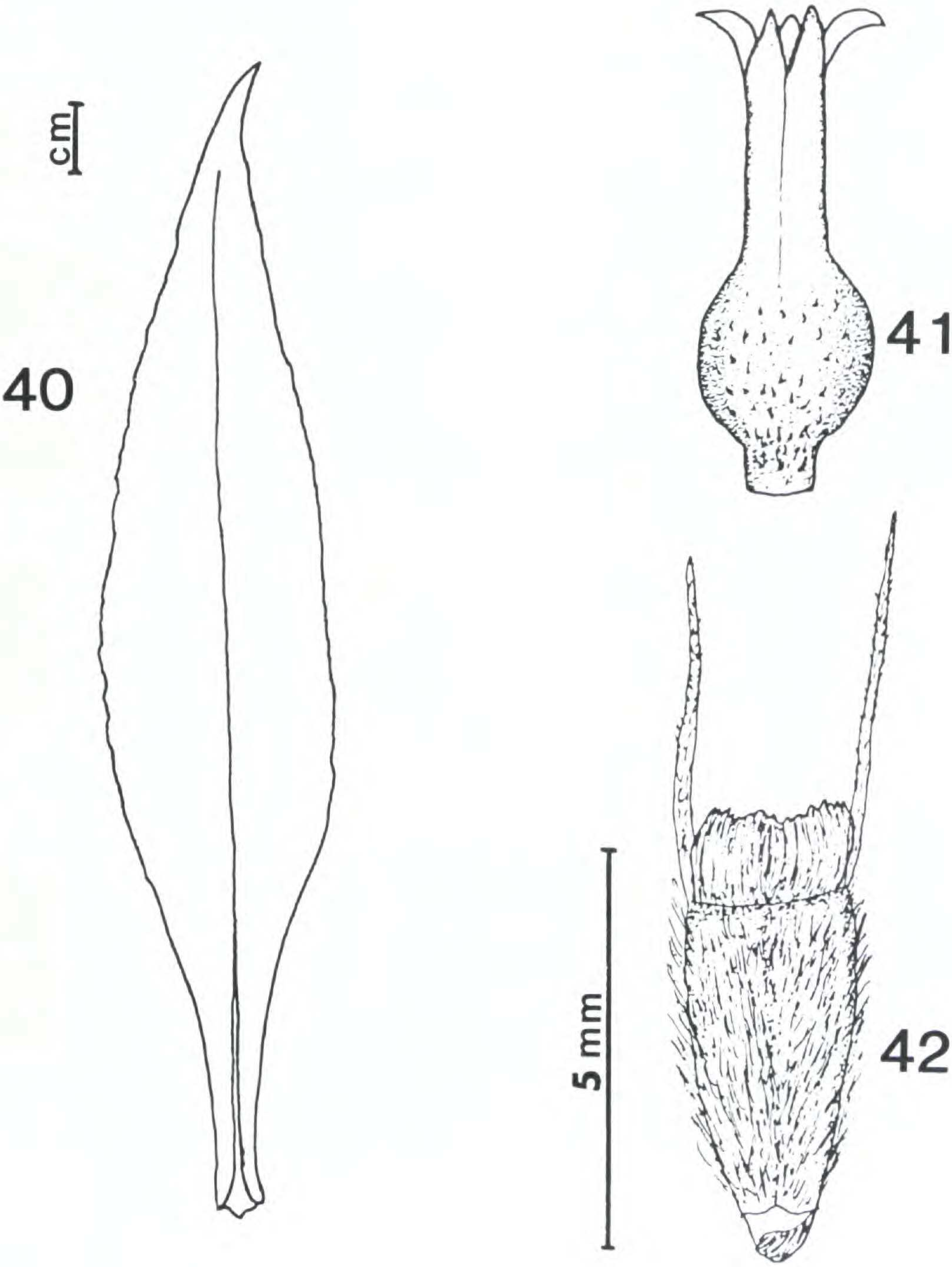
Saucito, *Gentry 703M* (MICH); canyon Narcissus, Río Mayo, *Gentry 1182* (F, MO); Dist. of Álamos, spring 1935, *Gentry s.n.* (NA); Curohui, Río Mayo, *Gentry 3645* (MO); 4 mi S of Mazocahui, *Turner 59-70* (ARIZ, OS, US); 1 mi S of Santa Ana, *McLaughlin 524* (ARIZ).

8. **Tithonia pedunculata** A. Cronquist, Mem. New York Bot. Gard. **12:** 286. *Fig. 1.* 1965. TYPE: MEXICO, Oaxaca, 42 mi NW of Tehuantepec, ca. 2300 ft, *A. Cronquist 9684* (HOLOTYPE, NY!; ISOTYPES, F, GH!, MICH!, MO!, TEX!, US!). Figures 40–42.

Erect, perennial shrub, 1–3.2 m tall. Stems round, brown, usually glabrous. Leaves alternate, with petioles to 3 mm long or sessile; blades linear-lanceolate, 7.5–23.5 cm long, 1.5–5.0 cm wide, at apex acuminate, at base attenuate, on upper surface hispid, on lower surface hispid to villous, at the margin entire to weakly crenate. Peduncles 11–27 cm long, 2–9 mm diam, sparsely to moderately pubescent near the head. Heads usually solitary, heterogamous. Receptacle 10–12 mm diam. Phyllaries 22–32, three-seriate, graduated, linear; outer bracts 6–11 mm long, 2–4 mm wide, at apex acute, on abaxial surface minutely pubescent; inner bracts 14–18 mm long, 3.5–6 mm wide, at apex acute or rounded, on abaxial surface minutely pubescent toward apex. Pales striate, 11–14 mm long, 2.5–3 mm wide; apex acuminate, 5–6.5 mm long, usually with secondary lobes, minutely pubescent. Ray florets 13–15; ligules yellow, oblong, 21–31 mm long, 6–8.5 mm wide, at apex trifid; tube 1–1.5 mm long, 0.5–1 mm diam; pappus absent or some small scales; achenes one-seriate, triangular, white-tan, sterile. Disk florets 90–100; corollas yellow; corolla lobes 5, 0.75–1.5 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, cylindrical portion 2.5–3.5 mm long, 1–1.5 mm diam, with expanded portion 1.5–3 mm long, 1.5–2 mm diam; tube minutely pubescent, 0.5–1 mm long, 0.75–1 mm diam; anthers black, 3–5 mm long; styles 6–7.5 mm long; stigmas pappillate, 2–3 mm long; pappus a ring of fused squamellae with two awns; achenes fertile, quadrangular, black, 4.5–5 mm long, 1.75–2.5 mm diam, with eliasome at base. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: September-October.

DISTRIBUTION: Restricted to central Oaxaca, México in xeric habitats (Fig. 33).



Figures **40–42.** Leaf (**40**; *La Duke et al. 408;* OS), disk corolla (**41**; *La Duke et al. 408,* OS), and disk achene (**42**; *La Duke et al. 410,* OS) of *Tithonia pedunculata.* Figures 41 and 42 same scale.

Tithonia pedunculata is an attractive shrub known from Oaxaca, México. It is most closely related to *T. fruticosa* of Chihuahua, Durango, Sinaloa, and Sonora. *Tithonia pedunculata* has narrower phyllaries, branches above the base, sparse to moderate pubescence on leaves, and is limited in distribution. *Tithonia pedunculata* is also the only member of this section with pappus and an eliasome. Eliasomes have been shown to be important in dispersal of achenes of Compositae by ants (Nesom, 1981), but these taxa usually have epappose achenes. The dispersal mechanism of this taxon warrants further investigation.

REPRESENTATIVE SPECIMENS. MEXICO. **Oaxaca:** Isthmus of Tehuantepec, *Paray 222* (ENCB); along rte 190 ca 42 mi W of Tehuantepec, *King 2472* (MICH, TEX); along rte 190 ca 61 mi W of Tehuantepec, *King 2474* (DS, MICH, TEX); 2 mi S of El Camaron, *Breedlove 7168* (DS, MICH, MO, NY); hwy 190, 69 mi NW of Tehuantepec, *Lathrop 6723* (DS, RSA); ca 98 km NW of Tehuantepec, *Cronquist & Fay 10859* (ENCB, NY); 8 mi W of Las Minas, *Wunderlin et al. 841* (MO); .9 mi NW Las Majadas on hwy 190, *La Duke & Jansen 408** (OS); 41.3 mi NW Tehuantepec on hwy 190, *La Duke & Jansen 409** (OS); 3 mi NW of Las Minas on rte 190, *La Duke & Jansen 410* (OS); ca 38 mi SE of Totolapan on rte 190, *Stuessy & Gardner 4276* (OS); 4.3 mi N of Las Animas on rte 190, *La Duke et al. 508* (OS); 6 mi N of bridge over Río Cameron, hwy 190, *Jansen & Harriman 500* (OS).

II. *Tithonia* section *Mirasolia* (Sch.-Bip. in Seemann) La Duke. Rhodora **84:**141. 1982.

Tithonia Gmelin subgen. *Mirasolia* Sch.-Bip. in Seemann Bot. Voyage Herald. 305. 1856.

Perennial shrubs; leaves linear to ovate, usually sessile to short-petiolate, margins serrate to crenate; phyllaries 3–4 (–5)-seriate; disk achenes rounded-quadrangular, epappose, glabrous, with eliasome at base. Species 9–11. TYPE SPECIES: *Tithonia calva* Sch.-Bip. in Seemann.

9. **Tithonia calva** Sch.-Bip. in Seemann, Botany Voyage Herald. 305. 1856.

Erect, perennial, shrub, 0.5–3 m tall. Stems round, tan, brown, to 2 cm diam, sparsely pubescent to villous with hairs 15 mm long. Leaves alternate, sessile; blades linear-lanceolate, ovate-lanceolate, to rounded triangular, 5.7–32.5 cm long, 1.1–17 cm wide, at apex acuminate, at base attenuate, auriculate, on upper and lower surface sparsely to densely pubescent, at margin serrate to crenate. Peduncles 5.5–15.5 cm long, 2–13 mm diam, moderately hispid to woolly near head. Heads usually solitary or in small clusters, heterogamous. Receptacle 6–14 mm diam. Phyllaries 16–29, three-(four)-seriate, graduated, linear to lanceolate; outer bracts 5.5–14 mm long, 1.5–3.5 mm wide, at apex acute to acuminate, on abaxial surface hispid-pilose, occasionally indurate below; inner bracts 6.5 mm long, 1.5–5 mm wide, at apex rounded to acute, on abaxial surface hispid-pilose. Pales striate, 5–10 mm long, 1.5–3.5 mm wide; apex aristate to acute, 0.5–3 mm long, with or without lateral lobes, minutely hispid towards apex. Ray florets (8–) 11–18; ligules yellow, linear to oval-oblong, 17–40 mm long, 4–12 mm wide, at apex trifid; tube 1–2 mm long, 0.5–1.5 mm diam; pappus absent; achenes one-seriate, white to yellow, sterile. Disk florets 60–140; corollas yellow; corolla lobes 5, 0.5–1 mm long, 0.5 mm wide, at the apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 1.5–4 mm long, 0.75–1.25 mm diam, with expanded portion 1–1.5 mm long, 1–2 mm diam; tube minutely pubescent, 0.5–11 mm long, 0.75–1.25 mm diam; anthers tan-brown or black, 3.5 mm long; styles 4.5–6.5 mm long; stigmas pappillate, 1.2–2.5 mm long; pappus absent; achenes fertile, black or mottled, rounded-quadrangular, 3–5 mm long, 1– 2 mm diam, with an eliasome at base. Chromosome number, $n = 17$.

9a. **Tithonia calva** Sch.-Bip. in Seemann, var. **calva.** Figs. 43–45.

Tithonia calva Sch.-Bip. in Seemann, Botany Voyage Herald. 305. 1856. TYPE: MÉXICO, Sierra Madre, *B. C. Seemann 2045* (HOLOTYPE, P [photo, OS!]; ISOTYPES, K! [photo, GH!]).

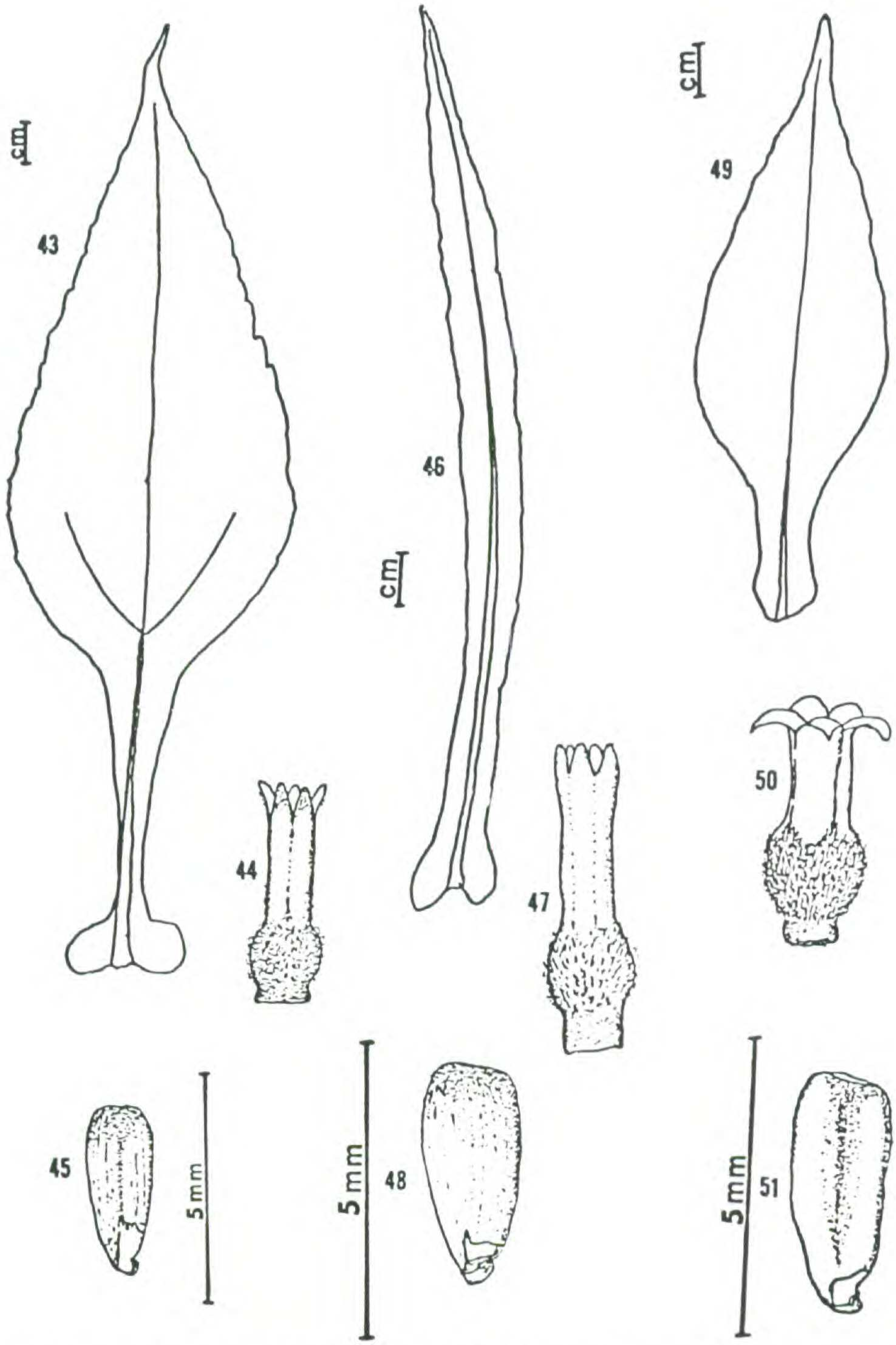
Mirasolia calva (Sch.-Bip. in Seemann) Benth. & Hook. ex Hemsl. in Godman & Salvin, Biol. Centr. Amer. Bot. **2:** 168. 1881.

Gymnolomia calva (Sch.-Bip. in Seemann) A. Gray, Proc. Amer. Acad. Arts **19:** 5. 1883.

Stems usually with long (to 15 mm) hairs. Leaves ovate-lanceolate to rounded-triangular, 9–32.5 cm long, 4–17 cm wide. Receptacle 10–14 mm diam. Disk florets 120–140.

PRINCIPAL FLOWERING TIME: August-November.

DISTRIBUTION: In the Mexican states of Chihuahua, Durango, Nayarit, Sinaloa. Fig. 22.



Figures **43–51.** Leaf, disk corolla, and disk achene of the three varieties of *Tithonia calva.* Leaf (**43**; *La Duke et al. 387*, OS), disk corolla (**44**; *Cronquist 10550*, MICH), and disk achene (**45**; *Cronquist 10550*, MICH) of *Tithonia calva* var. *calva.* Leaf (**46**; *La Duke et al. 430*, OS) disk corolla (**47**; *Gentry 5144*, ARIZ), and disk achene (**48**; *La Duke et al. 430*, OS) of *Tithonia calva* var. *auriculata.* Leaf (**49**; *Lamb 539*, DS), disk corolla (**50**; *McVaugh 23555*, US), and disk achene (**51**; *McVaugh 23555*, US) of *Tithonia calva* var. *lancifolia.* Figures 44 and 45 same scale; figures 47, 48, 50, 51 same scale.

Tithonia calva var. *calva* is readily distinguished by its epappose achenes and ovate to broadly lanceolate sessile auriculate-based leaves. The plants have been obtained primarily on Mexican Hwy 40 between Durango and Mazatlán in the high mountains, however, populations as far north as Chihuahua indicate it may be present throughout the western mountains, but in areas not readily accessible.

The most closely related species to *Tithonia calva* var. *calva* is *T. longiradiata*. These two taxa differ in a number of characteristics respectively, such as: 1) auriculate leaf base vs. attenuate, 2) linear to oblong phyllaries vs. spathulate phyllaries, and 3) distribution Northwestern México vs. Southeastern México, (Figure 22 vs 33).

REPRESENTATIVE SPECIMENS. MÉXICO. **Chihuahua:** Guasaremos Río Mayo, *Gentry 2900* (F, GH, K, MO, S, UC). **Durango:** 27.4 mi SW of Buenos Aires, *Ownbey & Ownbey 1884* (MICH); without locality, 15 Aug 1897, *Rose 2293* (GH); El Salto 3 km E of Sinaloa state line, *Detling 8598* (US); ca 3 km E of Sinaloa-Durango boundary on hwy from Villa Union, *Feddema 1822* (DUKE, ENCB, MICH); 1 mi above Revolcadero on hwy 40, *Weber & Charette 11799* (MICH); 1 mi W Revolcadero, *Flyr 300* (TEX); 2 mi NE of Durango-Sinaloa border along rte 40, *Torres 1775* (MICH); 1175 km post, hwy 40, *Walker 9* (NY); 1180 km post, hwy 40, May 1970, *Henze & Henze s.n.* (TEX); 87 mi E Mazatlán, hwy 40, *Reveal & Atwood 3619* (US); in Revolcadero on hwy 40, NW end of town, *La Duke et al. 385** (OS); 5.7 mi SE of Revolcadero on hwy 40, *La Duke 386** (OS). **Sinaloa:** 49 mi E of Villa Union, *Wiggins 13182* (DS); 2 mi NE of Revolcadero, *Waterfall 12728* (SMU); Palmito & vicinity, *Gentry & Arguelles 18183* (US); 22.1 mi E of Río Concordia at Concordia, rte 40, *Breedlove 1645* (DS, DUKE, MICH); Villa Union, *Van Den Bosch 64-2-1C* (UC); 15 km above Santa Lucia, *McVaugh 23586* (DS, DUKE, ENCB, LL, MICH, NY); 12 miles SW of El Palmito, *Cronquist 10550* (DS, ENCB, GH, MEXU, MICH, NY, US); La Lobera, *Hernandez 442* (LL); ca 27 mi E of hwy 15 on hwy 40, *Spetzman 1190* (NA); 13 mi SW el Palmito, *Webster & Brecken 15535* (GH, LL, MICH); Panuco, *Smith 183* (ARIZ); 6.8 mi NE of Santa Lucia on rte 40, *Keil & Canne 8845* (OS); along hwy 40 ca 8 mi W of Las Palmitas, *Norris et al. 20286* (DS); 1 mi SW of Santa Lucia along rte 40, *Roberts & Keil 10189* (OS, POM); Palmito, *Pinkava et al. P12913* (ENCB, OS); 2 mi before Potrerillos on rd from Mazatlán to Durango, *Kimmach & Sanchez-Mejorada 1646* (MEXU); Santa Rita on hwy 40, *La Duke 387** (OS); hwy 40 ca 33 mi NE of Concordia, *Hartman et al. 4297* (OS); 41 mi E Mazatlán, hwy 40, *Olsen & Lane 401* (ENCB, LL); Durango hwy at Barranca Liebre, *Ames 77-112* (ARIZ); .4 mi E of La Capilla del Taxte on hwy 40, *La Duke et al. 437** (OS); ca 38 mi E of jct of hwys 40 & 15, *Funk & Canne 3000* (OS).

9b. **Tithonia calva** var. **auriculata** (T. S. Brandegee) La Duke, *comb. et stat. nov.* Figures 46–48.

Gymnolomia auriculata T. S. Brandegee, Zoe **5:** 232. 1905. TYPE: MÉXICO, Sinaloa, Cofradia, Cerro Colorado, 5 Nov 1905, *T. S. Brandegee s.n.* (HOLOTYPE, UC!; ISOTYPES, GH!, POM!, US!).

Tithonia auriculata (T. S. Brandegee) S. F. Blake, Contr. Gray Herb. **54:** 9. 1918.

Stems glabrate to moderately pubescent. Leaves linear to linear-lanceolate, 13–16.5 cm long, 1.1–2.0 cm wide. Receptacle 6–9 mm diam. Disk florets 70–75.

PRINCIPAL FLOWERING TIME: October-December.

DISTRIBUTION: The Mexican states of Sinaloa and Sonora (Fig. 22).

Tithonia calva var. *auriculata* is easily distinguished by its epappose achenes and sessile, linear leaves. Its closest relative is *T. calva* var. *lancifolia* which tends to be similar in leaf morphology, but the ratio between length and width is usually greater than 8 to 1 in the former whereas it is less than 5 to 1 in the latter. Two populations of this taxon have unusual aristate-tipped pales *(La Duke et al. 430; Breedlove 35636),* but agree in all other features with the other populations of this taxon.

REPRESENTATIVE SPECIMENS. MÉXICO. **Sinaloa:** Mesa Malqueson, Cerro Colorado, *Gentry 5144* (MO); 15–20 km E of La Concordia above Copala, *Breedlove 35636* (MICH); 1.1 mi E of Chupaderos on rte 40, *La Duke et al. 430** (OS). **Sonora:** Quirocoba, dist. Álamos, *Gentry 772* (DS, MICH, SMU); Quirocoba, Rio Fuerte, *Gentry 2958* (LL); Sierra Tecurahui SE Sonora, *Gentry et al. 19361* (US).

9c. **Tithonia calva** var. **lancifolia** (B. L. Robinson & J. M. Greenm.) R. McVaugh, Contr. Univ. Michigan Herb. **9:** 443. 1972. Figures 49–51.

Gymnolomia calva var *lancifolia* B. L. Robinson & J. M. Greenm. Proc. Boston Soc. Nat. Hist. **29:** 103. 1899. TYPE: MÉXICO, **Nayarit,** Acaponeta, Feb 1895, *F. H. Lamb 539* (LECTOTYPE here chosen, US!; ISOLECTOTYPES, DS!, GH missing, MO!, NY!, US!). The GH specimen cited by S. F. Blake (1921) was not located (Canoso, *In litt.*).

Tithonia calva subsp. *lancifolia* (B. L. Robinson & Greenm.) S. F. Blake, Contr. U. S. Nat. Herb. **20:** 430. 1921.

Stems sparsely to moderately pubescent. Leaves linear-lanceolate to ovate-lanceolate, 5.7–16.5 cm long, 2.3–4.5 cm wide. Receptacle 7–9 mm diam. Disk florets 60–70 (–130).

PRINCIPAL FLOWERING TIME: January-April.

DISTRIBUTION: The Mexican states of Jalisco, Nayarit, Sinaloa, Sonora (Fig. 22).

Tithonia calva var. *lancifolia* is extremely variable and is most closely related to *T. calva* var. *auriculata,* but some populations approach the typical variety in many characters. It can be differentiated from *T. calva* var. *auriculata* by its lanceolate leaf shape and flowering time. Populations such as *Argulles 159* and *McVaugh 23555* approach *T. calva* var. *auriculata* most closely in leaf morphology.

REPRESENTATIVE SPECIMENS. MÉXICO. **Jalisco:** Las Mesitas SW of San Sebastian, *Mexia 1893* (BM, DS, F, GH, MICH, MO, NA, NY, UC, US). **Nayarit:** Tepic, *Palmer 1975* (F, GH, MICH, NY, US); 6–12 km NE of Miramar rd to Jalcocotán, *McVaugh 23555* (DS, DUKE, ENCB, LL, MICH, US); km 19, hwy 200, S of Tepic, *Gibson & Gibson 2196* (ARIZ, ENCB, NY, RSA); 17.9 mi W of rte 15 on rd to Jalcocotán, *La Duke et al. 463* (OS). **Sinaloa:** San Ignacio, *Ortega 131* (MEXU); Capadero Sierra Taucuichamona, *Gentry 5543* (ARIZ, DS, GH, MICH, MO, NA, NY). **Sonora:** San Bernardo & vicinity, Curahui, *Arguelles 159* (LL, TEX, US); Sierra Chiribo Río Mayo, *Gentry 1384* (ARIZ, F, GH, MICH, MO, US).

10. **Tithonia longiradiata** (Bertol.) S. F. Blake, Bull. Torrey Bot. Club **53:** 217. 1926. Figures 52–54.

Helianthus longiradiatus Bertol. Novi. Comm. Acad. Sci. Onst. Bonon. **4:** 436. 1840. TYPE: GUATEMALA, **Sacatepequez,** Volcan de Agua, 7 Aug 1962, *G. L. Webster, K. Miller, & L. Miller 12844* (NEOTYPE, MICH!; ISOTYPES, F!, LL!, MO!). The holotype, GUATEMALA, Volcan de Agua, *no collector s.n.* at BOLO was destroyed in the war (D. Ubaldi, *in litt.*). The neotype collection comes from the same locality, is complete in critical features, and is housed in several major herbaria.

Tithonia scaberrima Benth. in Örsted, Viden. Medd. Natur. For. Kjob. 9. 1852. TYPE: NICARAGUA, Segovia, vicinity of Chinotega coniferous region, 5000 ft, Jan 1848, *A. S. Örsted s.n.* (HOLOTYPE, C! [photo, DS!, OS!, US!]; ISOTYPE, C!).

Tithonia platylepis Sch.-Bip. in Benth. & Hook. Gen. Pl. **2:** 368. 1867. *Nom. nud., pro syn.* Based on specimen in "Pl. Lieb. exs." which was not specified.

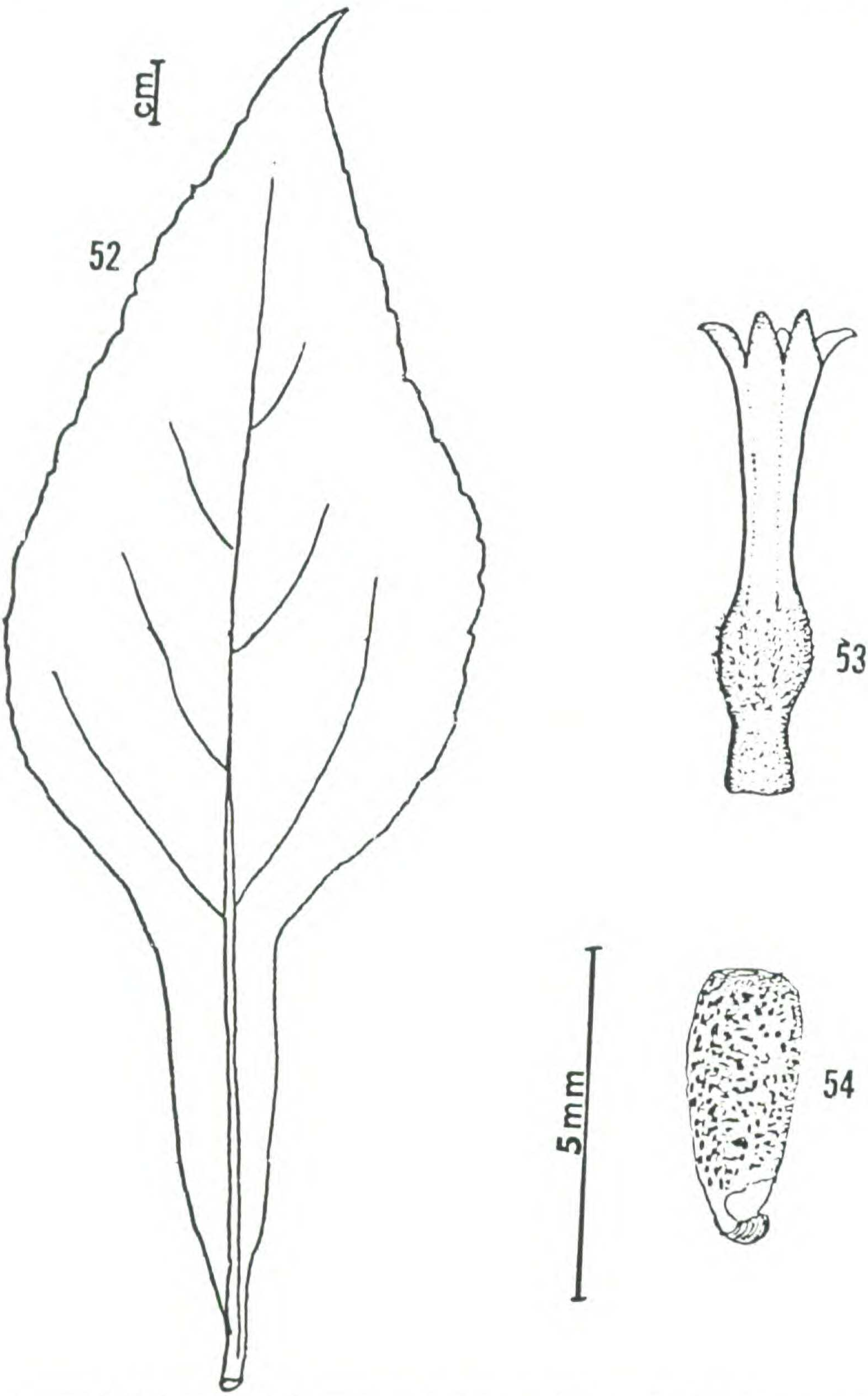
Mirasolia scaberrima (Benth. in Örsted) Benth. & Hook. ex Hemsl. in Godman & Salvin. Biol. Centr. America Bot. **2:** 168. 1881.

Gymnolomia platylepis (Sch.-Bip.) A. Gray, Proc. Amer. Acad. Arts **19:** 5. 1883. Invalid name, based on *nomen nudum, T. platylepis* Sch.-Bip. in Benth & Hook.

Gymnolomia decurrens Klatt, Leopoldinia **23:** 90. 1899. TYPE: MÉXICO, *C. Sartorius s.n.* (Holotype, not found). *Gymnolomia platylepis* (Sch.-Bip.) A. Gray according to Klatt in a manuscript note (Robinson & Greenman, 1899).

Perimeniopsis perfoliata Sch.-Bip. in Klatt. Leopoldinia **23:** 90. 1899. *Nom. nud., pro syn.* of *Gymnolomia decurrens* Klatt.

Tithonia glaberrima [incorrectly attributed to Hemsl. by] O. Kuntze, Rev. Gen. Pl. **1:** 371. 1891. *Orthogr. var.*



Figures **52–54.** Leaf (**52;** *La Duke et al. 515*, OS), disk corolla (**53**; *Cronquist & Sousa 10476*, TEX), and disk achene (**54**; *Cronquist & Sousa 10476*, TEX), of *Tithonia longiradiata.* Figures 53 and 54 same scale.

Gymnolomia pittieri Greenm. Proc. Amer. Acad. Arts **39:** 101. 1903. TYPE: COSTA RICA, "Bords du Rio Ceibo a Buenos Aires," 200 m, Feb. 1891, *H. Pittier 3735*. (LECTOTYPE: GH!, ISOLECTOTYPES, BR!, CR!).

Gymnolomia scaberrima (Benth. in Örsted) Greenm. Field Col. Mus. Publ. **126.** Bot. Ser. **2:** 268. 1907.

Tithonia pittieri (Greenm.) S. F. Blake. Contr. Gray Herb. **54:** 9. 1918.

Erect, perennial, shrub, 1–3 m tall. Stems round, brown to green-brown, pilose to long hispid. Leaves alternate, with petioles to 10 mm long or sessile; blades triangular to ovate to long lanceolate, 8.5–23 cm long, 2.6–13.5 cm wide, at apex acuminate, at base attenuate to truncate, on upper surface scabrous, on lower surface scabrous to pilose, at margin serrate to crenate. Peduncles 2.5–11 cm long, 4–8 mm diam, hispid to villous near head, glabrous lower. Heads solitary, heterogamous. Receptacle 10–14 mm diam. Phyllaries 24–28, four(-five)-seriate, graduated, spathulate; outer bracts 8.5–11 mm long, 3–6.5 mm wide, at apex acuminate, on abaxial surface villous; inner bracts 11–19 mm long, 2.5–6 mm wide, at apex acute to rounded, on abaxial surface minutely hispid. Pales striate, 8–10 mm long, 2–2.5 mm wide; apex acute, 1.5–4 mm long, usually with secondary lobes, minutely pubescent apically. Ray florets 13–30; ligules yellow, oblong, 31–37 mm long, 4.5–8 mm wide, at apex trifid; tube 1.5–2 mm long, 0.75–1 mm diam; pappus absent; achenes one-seriate, white-yellow, sterile. Disk florets 100–200; corollas yellow; corolla lobes 5, 1 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 2.5–4 mm long, 1–1.5 mm diam, with expanded portion 0.75–1 mm long, 1–1.5 mm diam; tube minutely pubescent, 0.75–1 mm long, 0.75–1 mm diam; anthers black, 3.5–4.5 mm long; styles 7.5 mm long; stigmas pappillate, 1.5–2.5 mm long; pappus lacking; achenes fertile, black, mottled, rounded quadrangular, 3–4 mm long, 1–2 mm diam, with eliasome at base. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: November-March.

DISTRIBUTION: Xeric areas of east-central México, south to Panama (Fig. 33).

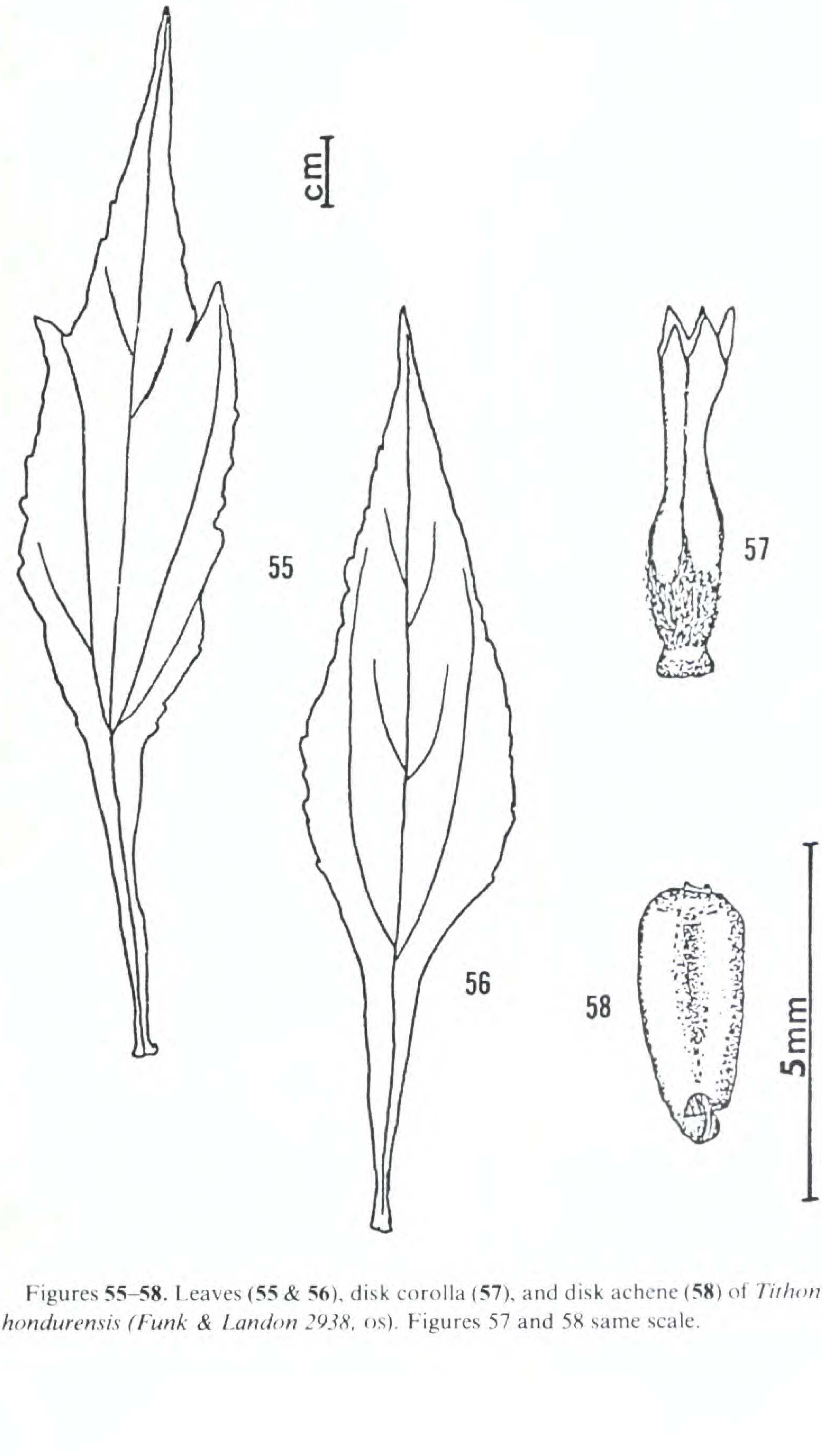
Tithonia longiradiata is a large shrub most closely related to *T. hondurensis*. It differs in its larger leaves, larger heads, more pubescent peduncle, and non-revolute leaf margin. In some collections of this taxon only upper leaves were collected and their size approached that of *T. hondurensis* but they lack the characteristic revolute margin of the latter species.

REPRESENTATIVE SPECIMENS. COSTA RICA. **Puntarenas:** Ujarras de Buenos Aires, *Pittier 10631* (CR). EL SALVADOR. **Morazán:** Montes de Cacaguatique, *Tucker 730* (K, LL, MICH, NY, UC, US). **San Vicente:** Volcan de San Vicente, *Standley 21500* (GH, NY, US). GUATEMALA. **Alta Verapaz:** Coban, *Turckheim 2053* (C, F, GH, LL, MICH, MO, NY, US). **Baja Verapaz:** 15 kms N of Salama near Pantin, *Williams et al. 42141* (F). **Chimaltenango:** near Tecpam, *Skutch 718* (DS, GH, LL, MICH, US); 14.6 mi E of 116 km post on rte ca-1, *La Duke et al. 534* (OS). **Guatemala:** 3.5 mi E of San Lucas, rte ca-1, *La Duke et al. 532** (OS). **Huehuetenango:** 24 mi NW Huehuetenango rte ca-1, *La Duke et al. 536* (OS). **Peten:** La Libertad, *Aguilar 472* (MICH, MO, NA, US). **Progreso:** Zanarate and El Chato bridge, *Molina and Molina 24926* (F, NY, US). **Queretaro:** rte 95, ca 10 mi S Quezaltenango, *King 3428* (DS, MICH, NY, TEX, US). **Quezaltenango:** Volcan Santa María de Jesús, hwy 95, *Stuessy & Gardner 4340* (OS). **Quiche:** Nebaj, *Skutch 1886* (F, GH, LL, NY, US). **Sacatepequez:** slopes of Volcan de Agua S of Santa María de Jesús, *Standley 59434* (F). **San Marcos:** S of San Marcos toward Castalia, *Williams et al. 26162* (F). **Solola:** San Lucas, 24 Jan 1907, *Kellerman sn* (OS). HONDURAS. **Copan:** between land de La Puerta & El Salto, *Pittier 1854* (F, US). **El Paraiso:** trail Danli to Finca La Enllia, *Carlson 2567* (F, MICH, UC). **Morazán:** entre Pena Blanca y lo de Ponce, *Williams & Molina 17109* (GH).

MÉXICO. **Chiapas:** S of Nicolas Montecristo, *Matuda 1957* (F, GH, MEXU, MICH, MO, NY, US); 8 mi W of San Cristobal de las Casas, *Cronquist & Sousa 10476* (DS, DUKE, ENCB, GH, MICH, NY, TEX, US); Tenejapa, *Ton 570* (DS, ENCB, GH, LL, NY); 3.7 mi E of rd to Apaz on rt 190, *La Duke et al. 515** (OS); 4.1 mi S Trinitaria, rte 190, *La Duke et al. 537* (OS). **Hidalgo:** Chalpulhuacan, *Cottam 10525* (ARIZ); rte 85, 5 mi SW of Hidalgo San Luis Potosí border, *King 4232* (F, MICH, NY, TEX, UC, US). **Oaxaca:** vicinity of Totentepec, *Nelson 772* (US). **Puebla:** km 8 de la Carr, que Baja a la Mina el Paraiso v Juarez, *Sarukhan et al. 1218* (MEXU). **San Luís Potosí:** mtns along rt 120 about 6 mi W of Xilitla, *King 4435* (MICH, NY, TEX, UC, USF). **Veracruz:** Fortin, *Kerber 327* (C, MICH, US); hill of Borregolorizaba, *Pringle 6087* (GH, MEXU, MO, NA, NY, UC, US); Zacuapam, *Purpus 2183* (F, GH, MO, NY, UC, US); El Durzano, San Juan Coscomatepec, *Ventura 4863* (DS, ENCB, MICH, RSA, TEX). NICARAGUA. **Jinotega:** vicinity of Jinotega, *Standley 9882A* (F).

11. **Tithonia hondurensis** La Duke Rhodora **84:** 139. 1982. TYPE: HONDURAS, **El Paraiso,** 5 mi W of dirt rd to Ojo de Agua and highway from Danli to Zamorano (hwy 4), 4 Dec 1978, *V. A. Funk, K. Landon 2938** (HOLOTYPE, OS!; ISOTYPE, F!, NY!). Figures 55–58.

Erect, perennial, shrub, 0.5–4 m tall. Stems round, tan to brown, moderately hispid to glabrous. Leaves alternate, sessile or with petioles to 4 mm long; blades linear to linear-lanceolate, occasionally



Figures **55–58.** Leaves (**55** & **56**), disk corolla (**57**), and disk achene (**58**) of *Tithonia hondurensis (Funk & Landon 2938,* OS). Figures 57 and 58 same scale.

with two small lobes at base, 6.5–23 cm long, 1.5–2.8 cm wide, at apex acuminate, at base attenuate to rounded attenuate, on upper surface short pubescence, densely puberulent, on lower surface longer, tomentose, at margin entire to serrate or crenate, revolute. Peduncles 8.5–25 cm long, 3–7 mm diam, sparsely to moderately hispid near head, reduced below. Heads usually solitary, heterogamous. Receptacle 10–15 mm diam. Phyllaries 20–23, four-seriate, graduated, linear to spathulate; outer bracts 4.5–8 mm long, 2–4 mm wide, at apex rounded, on abaxial surface slightly puberulent; inner bracts 7–11 mm long, 2–4 mm wide, at apex rounded, on abaxial surface glabrous. Pales striate, 6.5–9 mm long, 0.75–2 mm wide; apex acute, 0.5–1 mm long, with or without lateral lobes, minutely pubescent apically. Ray florets 13–15, neuter; ligules yellow, linear to ovate, 18–42 mm long, 6–10 mm wide, at apex trifid; tube 1–1.5 mm long, 0.5–.75 mm diam; pappus absent; achenes one-seriate, triangular, white. Disk florets 60–80; corollas yellow; corolla lobes 5, 0.75–1 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, cylindrical portion 2.5–3 mm long, 0.75–1 mm diam, expanded portion 1–2 mm long, 1 mm diam; tube minutely pubescent, 0.5–1 mm long, 0.5–.75 mm diam; anthers black, 3–4 mm long; style 5.75–7 mm long; stigmas pappillate, 1.5–1.75 mm long; pappus lacking; achenes fertile, black, rounded quadrangular, 3.5 mm long, 1.5 mm diam, with eliasome at base. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: November-March.
DISTRIBUTION: Belize and Honduras (Fig. 59).

Tithonia honduresis is a small shrub distributed locally in Belize Honduras and Honduras. It can be recognized easily by its small heads (receptacle 10–15 mm diam), and revolute leaf margins. Its closest relative is *T. longiradiata* from which it is distinguished by the above mentioned characteristics. This taxon has not been extensively collected, but the known range of morphological variation is quite great. Populations in Belize have the largest plants in all characters (e.g., *Spellman 1412*), while populations near Sigatepeque, Honduras are much smaller (e.g., *Molina 23298*). Characters of the secondary branches are also smaller than those on the main stem.

REPRESENTATIVE SPECIMENS. BELIZE. **Cayo:** *Hunt 295* (LL, BM); Makal River at end of Kinloch rd, *Spellman 1412* (MO). Vaca Falls: 1926, *Record sn* (OS). HONDURAS.

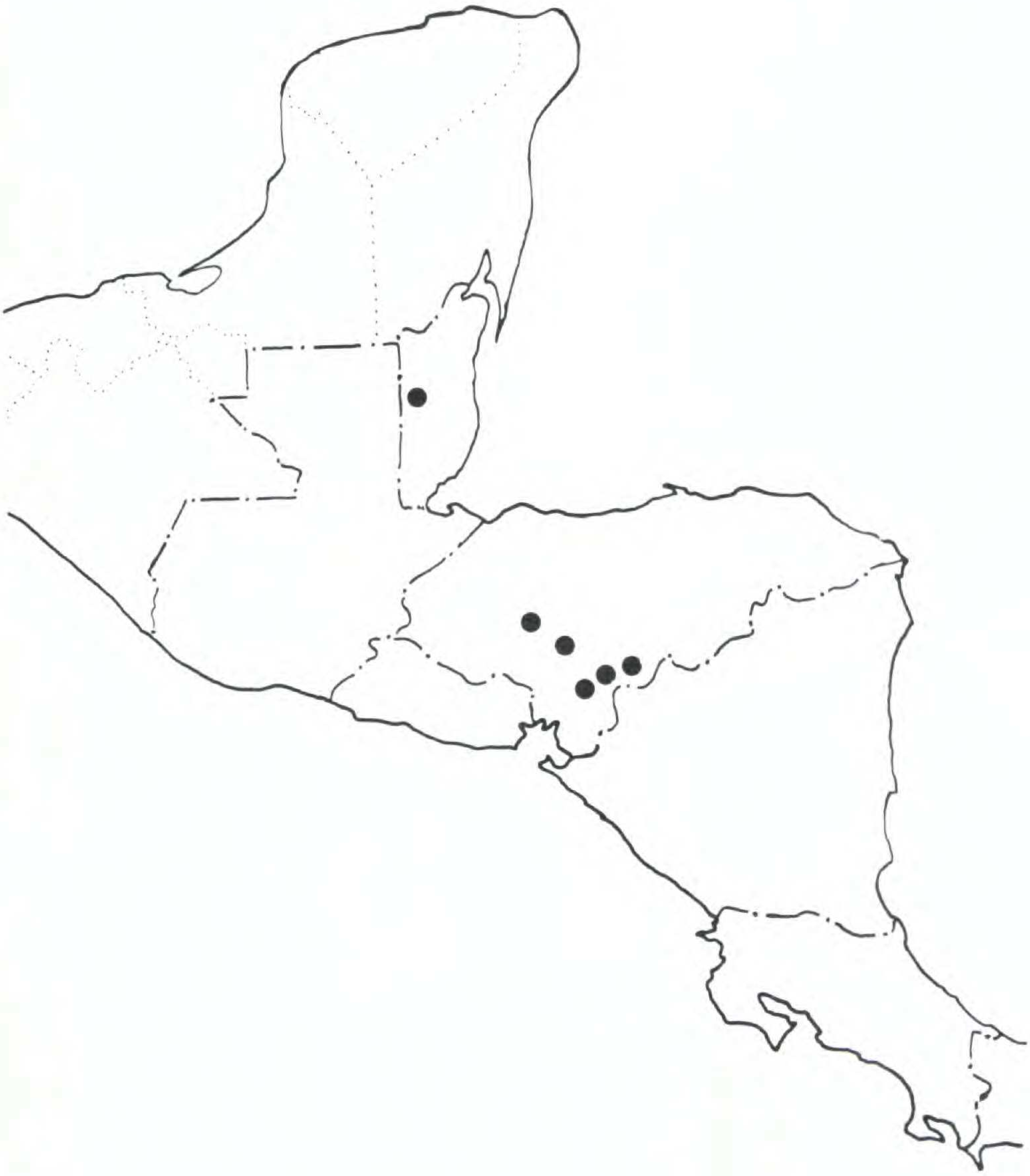


Figure **59**. Distribution of *Tithonia hondurensis* in Central America.

Comayagua: 3 km S of Siguqtepeque, *Molina 23298* (F, MO, NY, US); ca. 20 mi SE Comayagua on rte 1, *Stuessy & Gardner 4420** (OS). **El Paraiso:** Manzaragua rd, *Williams 11497* (F, GH, MEXU); Quebrada de Dantas on rd btwn Las Mesas & Yuscaran, *Standley 14984* (F); 8 km W of Ojo de Agua, *Williams 14750* (F); 8 km N of Yuscaran, *Williams & Williams 18655* (F, GH, LL, US); NE of Danli, *Molina 7599* (F); in Pine Forest of Guayabillas Road to Ojo de Agua, *Molina 25904* (DUKE, F, MO, NY, US).

DOUBTFUL AND EXCLUDED TAXA

Tithonia angustifolia Hook. & Arn. Botany Beechy Voyage 435. 1841. TYPE: MÉXICO, **Nayarit,** between San Blas and Tepic, *A.*

Sinclair s.n. (Holotype, K [photo, F!]). =*Viguiera angustifolia* (Hook. & Arn.) S. F. Blake, Proc. Amer. Acad. Arts **19:** 5. 1883.

Tithonia agrophylla D. C. Eaton in S. Watson, U.S. Geol. Exp. 40th Par. Bot. **5:** 423. 1871. TYPE: Location and date unknown, *E. Palmer s.n.* (HOLOTYPE, YU! on two sheets; ISOTYPE US!). =*Enceliopsis agrophylla* (D. C. Eaton in S. Watson) A. Nelson, Bot. Gaz. **47:** 433. 1909.

Tithonia decurrens A. Gray, Mem. Amer. Acad. Arts. Ser. 2. **4:** 85. 1849. TYPE: MÉXICO, **Chihuahua,** on the Bufa, Oct, *F. A. Wislizenus 193.* (HOLOTYPE, GH!). =*Viguiera decurrens* (A. Gray) A. Gray, Proc. Amer. Acad. Arts **19:** 5. 1883.

Tithonia excelsa (Willd.) DC. Prodr. **5:** 585. 1836. =*Helianthus excelsus* Willd. Sp. Pl. **3:** 2243. 1804. TYPE: location, date and collector unknown (HOLOTYPE, not found) =*Viguiera excelsa* (Willd.) B. & H. ex Hemsl. Biol. Centr. Amer. **2:** 177. 1881, fide Blake (1918). Identity based on plate 219 of *H. giganteus* Cav. Icon. **3:**10. 1795 which is a later homonym.

Tithonia glutinosa Hook. & Arn. Botany Beechy Voyage. 33. 1841. *pro. syn., nom. nud.*

Tithonia humilis (L.) O. Kuntze, Rev. Gen. Pl. **2:** 552. 1891. =*Rivina humilis* L. Gen. Pl. **1:** 121. 1753.

Tithonia ovata Hook. Bot. Mag. *t. 3901.* 1841. TYPE: MÉXICO, cultivated at Kew Gardens. (HOLOTYPE, K). =*Lasianthaea helianthoides* DC. Prodr. **5:** 608. 1836. Identification made from figure (*t. 3901*), and confirmed by Becker (1977).

Tithonia pachycephala DC. Prodr. **5:** 585. 1836. TYPE: MÉXICO, Guanajuato, 1829, *Mendez s.n.* (HOLOTYPE, G-DC, IDC *800, 949:* I. I!, Photo F!). =*Viguiera pachycephala* (DC) Hemsl. Biol. Centr. Amer. Bot. **2:** 178. 1881.

Tithonia pusilla A. Gray, Proc. Amer. Acad. Arts **5:** 124. 1861. TYPE: PERU, Obrajillo, *W. Rich s.n.* (HOLOTYPE, GH; ISOTYPE, US!). =*Viguiera pusilla* (A. Gray) S. F. Blake, Contr. Gray Herb. **54:** 162. 1918.

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